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REVISION OF THE VENOMOUS SNAKES OF BOLIVIA: PART 1.
THE CORALSNAKES (ELAPIDAE: *MICRURUS*)MICHAEL B. HARVEY¹,
JAMES APARICIO E.², AND
LUCINDO GONZALEZ A.³

ABSTRACT

Ten species of coralsnakes are known from Bolivia, and the ranges of an additional four approach Bolivia's northeastern border. Ranges of several species are expanded to accommodate recently collected material. Coralsnakes with characteristics thought to be diagnostic of *Micrurus tricolor* do not occur in Bolivia, and this species is considered to be a junior synonym of *Micrurus pyrrhocryptus*. *Micrurus frontifasciatus* is returned to the synonymy of *M. lemniscatus*. Some specimens previously referred to *M. frontifasciatus* are described as the new species *Micrurus serranus*, which is apparently restricted to dry intermontane valleys of the Andes above 1200 m. Putative subspecies of *M. spixii* occur in sympatry within Bolivia and differ from one another by a suite of morphological characters. Accordingly, we recognize *M. spixii* and *M. obscurus* as distinct species. Characteristics used to define *M. s. princeps* appear to be clinal, and this taxon is considered to be synonymous with *M. obscurus*. *Micrurus corallinus*, *M. ibiboboca*, and *M. tschudii* do not occur in Bolivia, despite earlier reports to the contrary. Claims that melanism increases with age in some species are not supported by our observations.

KEY WORDS: Bolivia, *Micrurus*, systematics

INTRODUCTION

In 1989, Campbell and Lamar observed that, "biologically, Bolivia is very poorly known, and the distributions of dangerously venomous snakes within this country are not well understood" (p. 78). Their book, *The Venomous Reptiles of Latin America*, was a seminal publication in Neotropical herpetology and stimulated extensive research in the systematics of Neotropical pitvipers and coralsnakes. In anticipation of the second edition of this book, we began a review of Bolivia's coralsnakes.

Until recently, scientific collecting in Bolivia has been sporadic, and Bolivia's coralsnakes have never been reviewed comprehensively. Nonetheless, Bolivia contains three endemic coralsnakes, and one of these, *Micrurus diana*, was described as recently as 1983 (Roze, 1983). With the exception of *M. frontifasciatus*, Schmidt and Roze have reviewed the Bolivian species throughout their ranges in South America and Jorge da Silva and Sites have reviewed the members of the *M. frontalis* complex. These studies contained few or no Bolivian specimens, and the authors were led to a few erroneous conclusions because of limited samples.

In the 1990s, Bolivian herpetology underwent a renaissance as several groups of European, American, and Bolivian herpetologists began systematically survey-

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ing the reptiles and amphibians throughout the country. During this period, Bolivian museums amassed substantial holdings of several rare coralsnakes. Our report draws heavily on this new material.

MATERIALS AND METHODS

In the accounts, a dash is used for ranges, whereas a slash (/) is used to separate counts from opposite sides of the same specimen. Wherever ranges appear, they are followed by means \pm standard deviation. Specimens were frequently damaged, and we follow each range or character frequency with the sample size.

Except for CBF (Colección Boliviana de Fauna, La Paz, Bolivia) and NK (Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz, Bolivia), institutional abbreviations are as listed in Leviton et al. (1985). Our synonymies are abbreviated in the sense that they only include references consulted during the preparation of this manuscript. Where identifications may have been in doubt, we verified actual specimens on which the citations are based.

For this study, we examined characters used in recent phylogenetic and taxonomic reviews of New World Elapidae. We routinely scored characters known to vary in some species (supralabial-prefrontal contact, supralabial number, supralabials entering orbit, temporal number, postocular number, and infralabial number) and features (frontal width, supraocular width, anal divided or entire) thought to be autapomorphies in a few species, such as an entire anal plate in *Micrurus hemprichii* and a narrow frontal in *M. surinamensis*.

We counted the number of infralabials contacting the chinshields and the number of gulars in a straight line from the last chinshield (two in coralsnakes) to the first preventral. Our definitions of preventrals and ventrals are consistent with the methodology of Dowling (1951). Therefore, our ventral counts cannot be directly compared to those of Schmidt, who routinely included number of gulars and preventrals in his ventral counts. A pair of postanal scales was included in subcaudal counts if the two sides were in contact or fused medially. We noted the number and location of entire and divided subcaudals.

We measured snout-vent length and tail length with a string and meter stick to the nearest 1 mm. Dial calipers or an ocular micrometer were used to measure head length (from the posterior margin of the last supralabial to the center of the rostral), greatest eye diameter, eye-nostril distance (from the anterior corner of the eye to the center of the nostril), greatest frontal width, and greatest supraocular width.

Among coralsnakes, pattern characteristics are particularly effective for diagnosing species. Except for *Micrurus annellatus* and *M. narduccii*, all Bolivian coralsnakes possess a tricolored triad pattern (Savage and Slowinski, 1992). We counted the number of triads on the body and tail, scoring incomplete triads at the distal end of the tail as thirds. Relative sizes of rings were quantified by counting vertebrals (i.e., the eighth row of dorsals) in the median triad. We did not measure ring lengths because number of vertebrals and ring length are redundant representations of the same character and because rings could not be easily measured on tightly coiled or twisted museum specimens. In all coralsnakes examined, individual triads were symmetrical with respect to ring length (see also Jorge da Silva and Sites, 1999). Consequently, we counted vertebrals in the red ring preceding the median triad, the median triad's first black and white or yellow rings, and the middle black ring. Distance to the first triad was expressed by

counting the number of vertebrals from the parietals to the first black ring on the body. Cephalic color (when not faded) and pattern were noted for each species. Amount of black pigmentation on the chin was scored as absent, diffuse, moderate, or heavy.

TAXONOMIC ACCOUNTS

Elapidae

Genus *Micrurus* Wagler, 1824

Definition.—*Micrurus* contains small (less than 700 mm) to large (up to 1.5 m), mostly secretive snakes with a pair of proteroglyphous fangs on the anterior end of the maxilla (Kardong, 1980) and with maxillary teeth absent behind the fang (Schmidt, 1928). The posterior part of the venom gland is inflected ventrally beneath the main body of the gland (Savitzky, 1978). The eye is relatively small and the pupil round or subelliptical. In all species, the snout is round in dorsal and lateral view, and the body is long relative to its width. The tail accounts for 4–20% of total length (Roze, 1996, provides a table of tail length/total length for most species of coralsnakes). With few exceptions, coralsnakes possess a dorsal color pattern consisting of red, yellow or white, and black rings (Savage and Slowinski, 1992).

Several authors (*inter alia*, Roze, 1996; Jorge da Silva and Sites, 1999; Slowinski, 1995) have called attention to the remarkably conservative arrangement of cephalic scales in coralsnakes. On the dorsal surface of the head, there are nine large supracephalic plates: two internasals, two prefrontals, two supraoculars, one frontal, and two parietals. Usually, one preocular, two postoculars, seven supralabials, and seven infralabials are present. A loreal scale is absent. Supralabials three and four enter the orbit except in *M. surinamensis*, where only supralabial four (rarely, only supralabial three) enters the orbit. The postoculars are followed by 0+1, 1+1, or 1+2 temporals. Relatively few gulars and preventrals separate two pairs of chinshields from the ventrals. Fifteen dorsals (17 in a few species) do not reduce in number anterior to the single (in *Micrurus hemprichii*) or divided anal plate. The subcaudals are usually divided; however, the first few (up to about the twelfth) are commonly entire in some species.

Boulenger assigned considerable taxonomic weight to contact of the mental and chinshields, and he used this character to diagnose some species such as *Elaps simonsi* (= *Micrurus pyrrhocryptus*) and *E. mentalis* (= *Micrurus mipartitus*). Similarly, this trait was used to distinguish *M. helleri* from *M. lemniscatus* (Schmidt, 1928). Fixation (or, at least, near fixation) of this trait is an apomorphy uniting the species sometimes referred to *Leptomicrurus*, and the trait occurs at low frequencies in several other coralsnakes (Amaral, 1926b; also see account for *M. serranus*, below). A similar case of polymorphism exists in some *Apostolepis* (Harvey, 1999).

The hemipenis is symmetrical, bilobed, noncapitate, and spinose. The *sulcus spermaticus* bifurcates proximal to the division of the lobes and extends centripetally along the lobes to the apices. A basal pocket bound medially and laterally by parallel folds is present on the asulcate side. The spines are largest near the base, diminishing in size distally. Terminal, spinelike awns are present in some species.

Content.—Phylogenetic analyses of coralsnakes have utilized morphology (Roze and Bernal-Carlo, 1987) and combined morphology, allozymes, and nue-

cleotides (Slowinski, 1995; Jorge da Silva and Sites, 2001). The results of Roze and Bernal-Carlo (1987) are difficult to evaluate because neither their characters nor their methodology are described except generally. Slowinski (1995) used clearly defined methods and recovered seemingly monophyletic clades of monadal and triadal coralsnakes. In his hypothesis, *Leptomicrurus* is nested within *Micrurus* as a basal lineage of the triadal clade. *Micrurus mipartitus* is sister to the monadal coralsnakes. Some species of Central and South American coralsnakes with a triad pattern appear to belong to the monadal clade; however, the species of this clade share a long tail and hemipenis. With the exception of *M. surinamensis*, the species of the "triadal" clade have short tails comprising 4.0–10.8% of total length in males, and species of the "monadal" clade have long tails comprising 10.0–18.5% of total length in males (Roze, 1996, his table 2). *Micruroides* (6.8–9.1% in males), *Leptomicrurus* (5.5–7.3% in males), and the *M. mipartitus* group (6.5–10.2% in males) also have short tails.

Romano (1972) synonymized *Leptomicrurus* with *Micrurus*. Although her conclusions were accepted initially by some authors (Roze, 1983; Campbell and Lamar, 1989), the genus is often recognized (Roze and Bernal-Carlo, 1987; Roze, 1996; Jorge da Silva and Sites, 2001). Here, *Leptomicrurus* is considered synonymous with *Micrurus*, because it is nested within the latter genus in Slowinski's (1995) phylogenetic hypothesis. Nonetheless, the three species commonly referred to this genus (*collaris*, *narduccii*, *scutiventris*) form a monophyletic group within *Micrurus* supported by at least two apomorphies: fixation of mental-chinshield contact (Schmidt, 1937) and strong inflection of the postero-ventral process of the venom gland (Slowinski, 1995; Roze and Bernal-Carlo, 1987; Savitzky, 1978).

Since the genus was last reviewed (Roze, 1996), Jorge da Silva and Sites (1999) partitioned the *Micrurus frontalis* complex and Campbell (2000) described a new species from Puebla, Mexico. Compelling evidence (Jorge da Silva and Sites, 2001) suggests that several taxa, notably *M. lemniscatus*, require further revision and the number of species is expected to increase. Including taxonomic changes made herein, *Micrurus* is one of the largest genera of Neotropical snakes and now includes 69 species: *M. albicinctus* Amaral, *M. alleni* (Schmidt), *M. altirostris* (Cope), *M. ancoralis* (Jan), *M. annellatus* (Peters), *M. averyi* Schmidt, *M. baliocoryphus* (Cope), *M. bernadi* (Cope), *M. bocourti* (Jan), *M. bogerti* Roze, *M. brasiliensis* Roze, *M. browni* Schmidt and Smith, *M. catamayensis* Roze, *M. circinalis* (Duméril, Bibron, and Duméril), *M. clarki* Schmidt, *M. collaris* (Schlegel), *M. corallinus* (Merrem), *M. decoratus* (Jan), *M. diana* Roze, *M. diastema* (Duméril, Bibron, and Duméril), *M. dissoleucus* (Cope), *M. distans* (Kennicott), *M. dumerilii* (Jan), *M. elegans* (Jan), *M. ephippifer* (Cope), *M. filiformis* (Günther), *M. frontalis* (Duméril, Bibron, and Duméril), *M. fulvius* (Linnaeus), *M. hemprichii* (Jan), *M. hippocrepis* (Peters), *M. ibiboboca* (Merrem), *M. isozonus* (Cope), *M. langsdorffi* Wagler, *M. laticollaris* (Peters), *M. latifasciatus* Schmidt, *M. lemniscatus* (Linnaeus), *M. limbatus* Fraser, *M. margaritifera* Roze, *M. medemi* Roze, *M. meridensis* Roze, *M. mertensi* Schmidt, *M. mipartitus* (Duméril, Bibron, and Duméril), *M. multifasciatus* (Jan), *M. multiscutatus* Rendahl and Vestergren, *M. narduccii* (Jan), *M. nebularis* Roze, *M. nigrocinctus* (Girard), *M. obscurus* (Jan), *M. ornatissimus* (Jan), *M. pachecogili* Campbell, *M. paraensis* Cunha and Nascimento, *M. peruvianus* Schmidt, *M. petersi* Roze, *M. proximans* Smith and Chrapliwy, *M. psyches* (Daudin), *M. putumayensis* Lancini, *M. pyrrhocryptus* (Cope), *M. remotus* Roze, *M. ruatanus* (Günther), *M. sangilensis* Nicéforo-María, *M. scutiventris* (Cope), *M. serranus* Harvey, Aparicio, and Gonzales, *M. spixii*

Wagler, *M. spurrelli* (Boulenger), *M. steindachneri* (Werner), *M. stewarti* Barbour and Amaral, *M. stuarti* Roze, *M. surinamensis* (Cuvier), *M. tschudii* (Jan).

KEY TO THE CORALSNAKES OF BOLIVIA

Coralsnakes have a remarkably conservative morphology, and characters of coloration are the most effective for identification of many species. In the key below, each couplet contains more than one character so that aberrant specimens can still be identified. In the diagnoses, characters are presented in a numbered and standardized format. We have arranged the characters so that they decrease in utility; i.e., the first few characters are more obvious and less prone to intra-specific variation than the last characters.

- 1. Dorsal pattern bicolored or tricolored, but rings not arranged in triads; tail long, more than 12% of snout-vent length in males *Micrurus annellatus*
- 1'. Dorsal pattern of tricolored triads or dorsum black with yellow or orange ventrolateral spots; tail short, less than 12% of snout-vent length in males 2
- 2 (1'). Dorsum black except for an orange (pale yellow in preservative) frontoparietal band; circular orange or yellow spots on venter; ventrals more than 260 in both sexes; mental contacting chinshields *Micrurus narduccii narduccii*
- 2'. Dorsal pattern of triads with or without frontoparietal band; ventrals almost always fewer than 260 (rarely more than 260 in *M. lemniscatus*); mental rarely contacting chinshields or contacting chinshields at low frequencies (e.g., in 5% of *M. serranus*) 3
- 3 (2'). Anal plate entire; dorsal pattern consisting of long black rings separated by short orange or white rings; dorsal surface of head black to level of parietals (orange); ventrals 156–191 (Campbell and Lamar, 1989) *Micrurus hemprichii*
- 3'. Anal plate divided or entire anal plate occurring at low frequencies (e.g., in 10% of *M. serranus*); rings on either side of middle black ring white or yellow, black rings usually shorter than red rings but may be more than five times as long as red rings in some specimens; ventrals more than 200 except in *Micrurus surinamensis* 4
- 4 (3'). One supralabial (usually the fourth) entering orbit; scales of head red, edged in black; ventrals fewer than 190 *Micrurus surinamensis*
- 4'. Two supralabials (usually 3 and 4) entering orbit; dorsal surface of head black, red, or yellow, but if lightly pigmented then heavily blotched with black or with black bands; ventrals more than 200 5
- 5 (4'). First triad incomplete, one or two black rings on neck (in some specimens with two black rings, location of “missing” ring may be visible as row of black scales lateral to parietals; some specimens from Colombia have complete ring overlapping parietal) 6
- 5'. First triad complete, separated from parietal tips by 1–12 red vertebrals 7
- 6 (5). First triad consisting of two black rings, the first greatly attenuated anteriorly and dorsally; scales of snout yellow with black blotches and margins, scales of parietal region red with black markings; black ocular band extending from supralabials 3–4 across supraoculars and frontal; exterior black rings usually shorter or incomplete ventrally *Micrurus obscurus*
- 6'. First triad consisting of one black ring with a near vertical anterior edge; dorsal head scales black with red margins; exterior black rings as long as white yellow rings or longest ventrally *Micrurus spixii*
- 7 (5'). White band crossing snout (except in rare, apparently aberrant specimens); specimens from Bolivian lowlands and humid Andean foothills also with white rings longest ventrally and usually some infralabials entirely black; specimens from dry Andean valleys also having first triad separated from parietals by 1–5 scales and parietals partially red 8
- 7'. Dorsal head scales black, edged in white or white with black edges but distinct white band across snout absent; white rings longest dorsally, often restricted ventrally; pigmentation of chin variable, but anterior infralabials not entirely black; first triad more than five dorsals behind parietals or first triad contacting parietal tips 9



Fig. 1.—*Micrurus annellatus* from Bella Vista, Itenez province, Beni. Photo by J. Padial.

- 8 (7). White rings longest and immaculate ventrally; edges of scales within white snout band uniformly white, not edged in black; snout bluntly rounded; eastern lowlands and mesic Andean foothills *Micrurus lemniscatus*
- 8'. White rings longest dorsally, constricted or interrupted by black rings ventrally; scales within white snout band edged in black; snout subacuminate; xeric, intermontane valleys of the Andes *Micrurus serranus*
- 9 (7'). First triad contacting or closely approximating parietals; scales of red rings immaculate or with weak black edges, black pigment in red rings considerably less than in white rings; some scales in white rings with heavy black apices, giving the impression of black blotches within white rings *Micrurus diana*
- 9'. Five or more red vertebrals separating first triad from parietals; scales of red rings with heavy black apices, at least posteriorly; considerably less black pigment in white rings than in red rings *Micrurus pyrrhocryptus*

Micrurus annellatus (Peters)
(Fig. 1)

Elaps annellatus Peters, 1871:402. HOLOTYPE male, "Pozuzu" =Pozuzo, Peru (ZMB 7185). Boulenger, 1896:418; Peracca, 1897a:7.
Elaps balzani Boulenger, 1898a:130. HOLOTYPE male, "Province Yungas, at an altitude of 1600

- meters" (MSNG 28874 fide Capocaccia, 1961). [The specimen came from the vicinity of Coroico (in present day La Paz department, Nor Yungas province) or Chulumani (La Paz, Sud Yungas) (Boulenger, 1898a, p. 128)].
- Elaps regularis* Boulenger, 1902b:402. HOLOTYPE female, "Chulumani, Bolivia, 2000 m" (BMNH 1946.1.17.22).
- Micrurus corallinus corallinus* (Merrem): Amaral, 1925:23 (in part); Amaral, 1926a:23 (in part); Amaral, 1930a:51–52 (in part); Fugler, 1986:57.
- Micrurus langsdorffii* Wagler: Schmidt, 1936:191 (in part); Schmidt and Walker, 1943:293.
- Micrurus balzani* (Boulenger): Schmidt, 1936:192; Schmidt and Walker, 1943:293.
- Micrurus annellatus* (Peters): Hoge and Romano, 1973:121; Duellman, 1979:456; Fugler, 1986:56; Fugler and Cabot, 1995:60.
- Micrurus annellatus annellatus* (Peters): Schmidt, 1954:323; Peters, 1960:530; Roze, 1967:6; Roze, 1970:202; Miyata, 1982:18; Roze, 1983:315; Carrillo de Espinoza, 1983:27; Campbell and Lamar, 1989:97; Golay et al., 1993:157; Carrillo de Espinoza and Icochea, 1995:19; David and Ineich, 1999:132.
- Micrurus annellatus montanus* Schmidt, 1954:322. HOLOTYPE male, "Camp 4, about 10 km. north of Santo Domingo Mine, Puno, Peru, at about 2000 m. altitude" (FMNH 40221). Roze, 1967:8; Carrillo de Espinoza, 1983:28.
- Micrurus annellatus bolivianus* Roze, 1967:7, figure 2. HOLOTYPE female, "Charobamba River, about 50 kilometers northeast of Zudañez, Chuquisaca, Bolivia" (ZMH 2706e). Roze, 1970:203; Hoge and Romano, 1973:121; Roze 1983:316; Campbell and Lamar, 1989:97; Golay et al., 1993:158; David and Ineich, 1999:132.
- Micrurus annellatus balzani* (Boulenger): Roze, 1967:6; Roze, 1970:203; Roze 1983:315; Campbell and Lamar, 1989:97; Golay et al., 1993:157; Carrillo de Espinoza and Icochea, 1995:19; David and Ineich, 1999:132.

Diagnosis.—(1) Dorsal pattern tricolored or bicolored but not consisting of triads; (2) hemipenis and tail relatively long; tail length 16.1–18.3% of snout-vent length in males; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) dorsal surface of head black except for strongly angled, yellow band crossing parietal tips, temporals, and posterior supralabials (5–6 and part of 7); (7) chin pigmentation variable.

Description.—(Based on 5 male, 1 female, and 1 unsexed juvenile museum specimens and photographs of an unsexed specimen from Beni). Although our sample is relatively small, the material exhibits noteworthy variation in several features and largely consists of specimens not available to earlier revisors of this species. Specimens we examined range from 185–545 mm in total length and are considerably shorter than the longest previously measured specimen, a female from southern Peru that was 728 mm (Schmidt, 1954). Sexual dimorphism is evident in body proportions and counts of ventrals and subcaudals. The tail is 16.1–18.3% (16.8 ± 1.0 , 4) as long as snout-vent length in males and 12.4% as long in the female specimen. Males have 187–199 (194 ± 5 , 4) ventrals and 38–45 (42 ± 3 , 4) subcaudals compared to 211 and 34 in the female. In NK 2047, the first three subcaudals are entire; all are divided in the other specimens. In all specimens, the anal is divided.

The head of males accounts for 2.1–2.4% (2.3 ± 0.1 , 3) of snout-vent length. Eye-nostril distance is 20.3–24.2% (21.7 ± 2.1 , 3) and eye diameter is 13.6–15.2% (14.4 ± 0.8 , 3) of head length in both sexes. All of our specimens have 7/7 supralabials, 3–4 entering the orbit; temporals are 1+1/1+1; the prefrontal does not contact the supralabials. Five of six specimens (83%) have 2/2 postoculars; CBF 490 has 1/1 postoculars. The prefrontals do not contact the supralabials, and the supraoculars are 52–86% (66 ± 15 , 4) as wide as the frontal. All specimens have 7/7 infralabials, the first pair separating the mental from the chin-

shields and the first four pairs contacting the first pair of chinshields. The chinshields are separated from the ventrals by three gulars and preventrals.

The dorsal surface and sides of the head are usually uniformly black except for the yellow nuchal ring. CBF 1586 possesses a circular yellow spot on the posterior edge of each supraocular. The yellow nuchal ring is longest on the sides of the head where it overlaps the temporals and supralabials 5–6 and part of 7. It shortens at the parietal tips where it overlaps the first vertebral and the posterior one to two-thirds of the parietals. In some specimens (NK 2047 and AMNH 2975), the mental and first three infralabials are black and the nuchal ring continues onto infralabials 4–5. The other specimens lack a uniformly black chin; rather, their mentals and anterior infralabials are yellow with moderate black pigment along the edges.

In our small sample, we did not observe increasing melanism with age; although the amount of black in the red rings varied from heavy (e.g., CBF 490, SVL 397 mm) to faint (photographed specimen and NK 2047, SVL 467 mm). The red coloration was completely obscured by black in the smallest specimen (AMNH 2975, SVL 330 mm) and clearly visible in the largest specimens (NK 2047, SVL 467 mm). Males have 20–25 (23 ± 2 , 4) black rings on the body and 6–8 (7 ± 1 , 4) black rings on the tail. The female specimen has 50 black and melanistic (?) red rings on the body and 6 black rings on the tail. The red rings are as long or longer than the black rings; at midbody, the red ring is 3–6 (4 ± 1 , 5), the black ring 2–4.5 (3 ± 1 , 5), and the yellow ring 1–0.5 vertebrals long. Except for the nuchal rings, the body and tail rings are not strongly angled. In FML 1045, the first five black rings on the body and the rings on the tail are complete; however, the other black body rings extend only as far as the paraventrals.

Slowinski (1995) reported a hemipenis extending only 4 subcaudals in USNM 193814 and questioned whether the specimen was anomalous considering that most species in the group had hemipenes extending 8–17 subcaudals. He seems to have been correct: in NK 2047, the hemipenis extends for 20 subcaudals and bifurcates at the level of the 10th subcaudal.

Distribution and Comparative Material.—As currently defined, this species ranges from the Cononaco River, Ecuador (Schmidt, 1954) to Chuquisaca, Bolivia (Roze, 1967). In Bolivia, specimens occur in the Andes and adjacent lowlands of La Paz, Pando, and Beni (Fig. 2). This species was included in the Colombian fauna by Amaral (1931), who did not cite a specimen upon which his record was based. Pérez-Santos and Moreno (1988) report this species from Leticia, Amazonas, Colombia, but no museum specimens are known from there (W. W. Lamar, personal communication).

BOLIVIA. BENI. Iténez: Bella Vista (photo only, Fig. 1). **Unknown:** (AMNH 2975–76, Paratypes of *M. annellatus montanus*). **COCHABAMBA. Carrasco:** 30 km N Monte Punco, Yungas de Totoras, Río Yanimayo (FML 1045). **LA PAZ. Iturrealde:** Yariapo (CBF 1586). **Nor Yungas:** Cotapata (CBF 1932). **Sud Yungas:** Irupana (CBF 490), “Tulimane” = Chulumani, 1800 m (USNM 98890). **PANDO. Federico Román:** “80 km de Cachuela Esperanza” (NK 2047). **UNKNOWN:** “Sierras de Bolivia” (FMNH 22588).

Remarks.—Some authors have suspected that variation in length of the pale parietal band (Roze, 1983) and presence or absence of red rings were partially attributable to ontogeny (Roze, 1983; Schmidt, 1954). Roze (1983) claimed that all specimens from the Peruvian Amazon up to 1000 m and two specimens from Beni (AMNH 2975–76) were white and black. Tricolored specimens were only known from higher elevations (Schmidt, 1954; Roze, 1983) where some adults from Peru and Bolivia retain the tricolor pattern. Without explanation, Roze

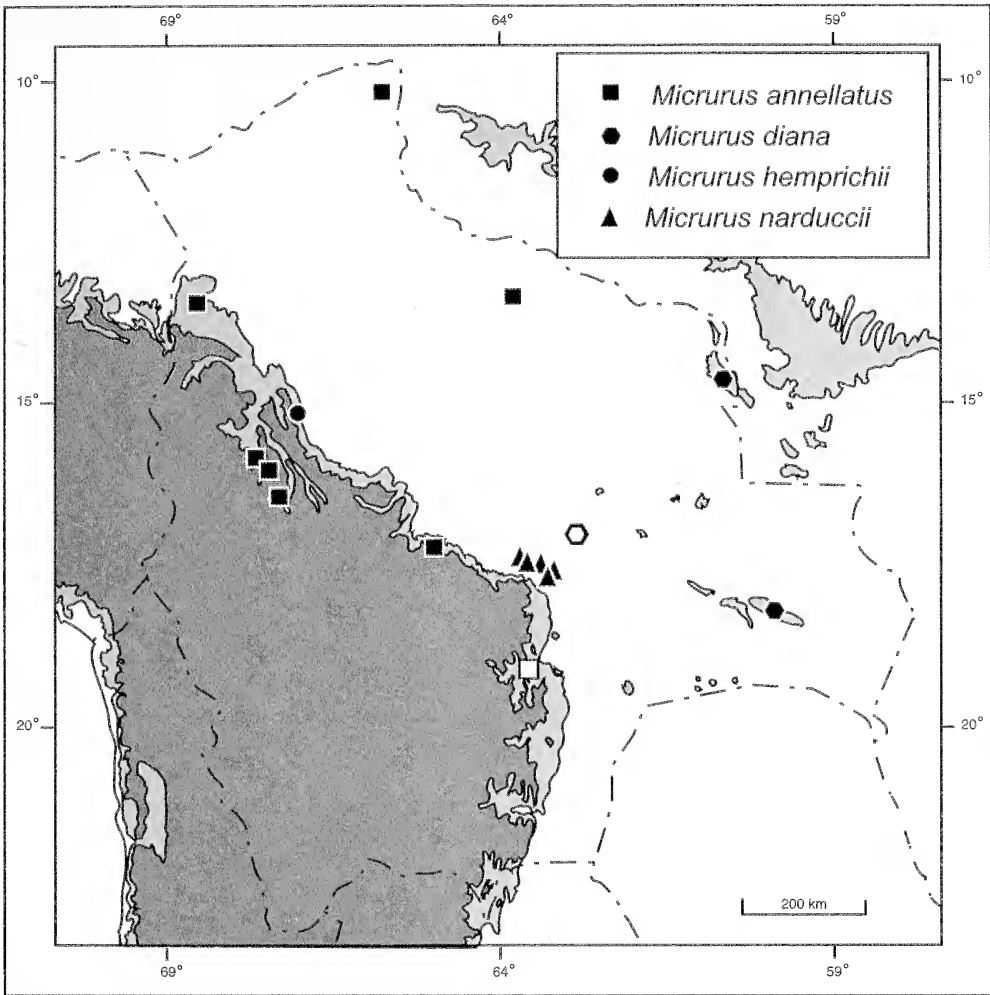


Fig. 2.—Distribution of four species of Bolivian coral snakes.

(1983) considered ZMH 5396 from San Carlos, Beni, to be an intergrade between the subspecies *balzani* and *annellatus*.

The large adult (SVL 476 mm) from the lowlands of Pando and the specimen illustrated in figure 1 from Beni both have red rings, contradicting claims that presence of red is correlated with ontogeny or elevation. Length of the pale parietal band shows little variation in Bolivian samples and does not appear to vary with age.

A strong case for recognizing subspecies of *Micrurus annellatus* has not been made. Roze (1996) recognizes three subspecies and separates them using number of postoculars, presence of red rings, and length of postocular ring. Using his key, CBF 490 is the only specimen with one postocular and keys to *M. annellatus balzani*. The remaining specimens key to *M. a. annellatus* because they have two postoculars and their parietals are one- to two-thirds black. Thus, if the two subspecies are valid, they occur in the same cloud forests along the slopes of the

Andes in La Paz and Cochabamba. It is unlikely that subspecies maintain their identity in sympatry, and we believe that number of postoculars is polymorphic within a single, monotypic species.

Micrurus diana (Roze)

(Fig. 3)

Micrurus frontalis diana Roze, 1983:324. HOLOTYPE male, "vicinity of Santiago, Provincia Chiquitos" Santa Cruz, Bolivia, 700 m (FMNH 159889). Campbell and Lamar, 1989:115; Golay et al., 1993:167.

Micrurus diana (Roze): Roze, 1994:179; Roze, 1996:152; Harvey, 1998:151, 353; Jorge da Silva and Sites, 1999:170; David and Ineich, 1999:136.

Diagnosis.—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad complete; (7) first triad contacting parietal tips; (8) parietals black with white edging; scales of snout either white with black edging or black with white edging (see remarks below); (9) scales of white rings edged in black and white rings with irregular black blotches; red rings nearly or completely immaculate; (10) white rings longest dorsally, constricted or broken ventrally by black rings; (11) chin mostly immaculate, red or red and white; (12) 9–11 triads on the body; (13) relative lengths of rings variable.

Remarks and Variation.—This species was described relatively recently (Roze, 1983) and a detailed redescription was provided by Jorge da Silva and Sites (1999). Since we do not have access to new material, we will only comment on some discrepancies between Jorge da Silva and Sites' (1999) diagnosis and the specimens we examined.

NK 219 and AMNH 120600 were also examined by Jorge da Silva and Sites (1999), but NK 219, in particular, violates key parts of their diagnosis of this species: (1) The dorsal snout scales (rostral, nasal, preocular, prefrontals, frontal) of NK 219 are black with white edges rather than white with black edges. Just the opposite is true for the other specimens. (2) In NK 219, the chin is red rather than white. White pigment is clearly present on the chinshields in the type specimens. (3) The white rings are shorter (2 vertebrals in the middle triad in NK 219) or as long as the middle black ring and shorter than the exterior black rings. Sites and Jorge da Silva (1999) characterize this species as having white rings longer than the black rings. In NK 219 and AMNH 120600, the black exterior rings are 4–4.67 vertebrals long and noticeably longer than the middle ring (3 vertebrals in both specimens). (4) Including the nuchal triad, AMNH 120600 (a male) and FMNH 195899 (a female) both have 9 body triads (including the triad on the neck, Fig. 3), rather than 10–11 (Jorge da Silva and Sites, 1999). To us, the differences between topotypic material and the specimen from Velasco Province are considerable, and the status of the population in the Parque Noel Kempff Mercado should be reconsidered when more material becomes available.

Micrurus diana may be synonymous with *Micrurus brasiliensis*. We tentatively recognize these species because their known distributions are distantly allopatric. Reference to their key and point-by-point comparisons of their diagnoses indicate that Jorge da Silva and Sites (1999) considered these species to be distinct on the basis of one character. *Micrurus diana* has more extensive black pigmentation on its parietal scales: black with white margins versus anterior and medial parts of parietals black in *M. brasiliensis*. *Micrurus diana* is known from only a few

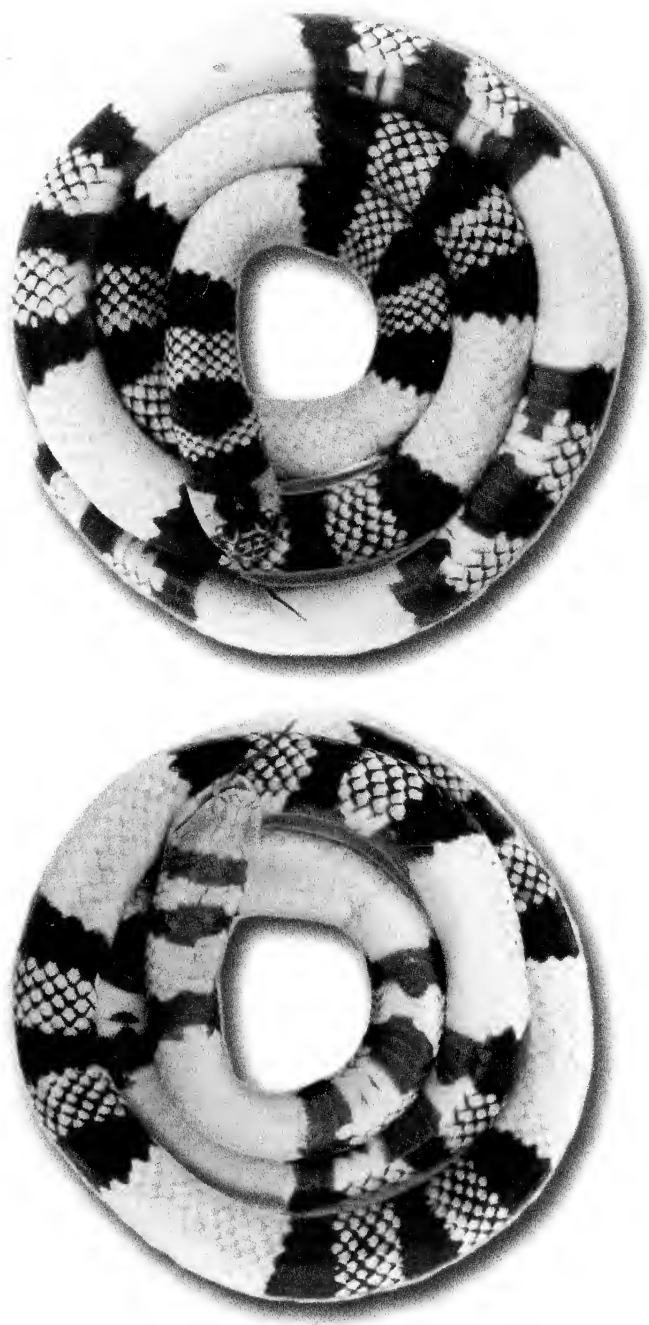


Fig. 3.—*Micrurus diana*, paratype (AMNH 120600 M, SVL 536 mm) from the vicinity of Santiago, Chiquitos, Santa Cruz.

specimens. On the other hand, *Micrurus serranus* may be closely related to the *M. frontalis* complex, and the amount of pigmentation on its parietals is highly variable. We do not place much confidence in this supposed difference between *M. brasiliensis* and *M. diana*. The morphometric analysis does not reveal differences between these species. Figure 2 in Jorge da Silva and Sites (1999) shows that the ranges and means of canonical variables 1 and 2 for *M. diana* are almost completely encompassed by the wider ranges for *M. brasiliensis*. Ranges for selected meristic and morphometric data tabulated in tables 1 and 2 of Jorge da Silva and Sites' publication overlap for these species. In both species, the first triad contacts the parietals in some or all specimens.

To published accounts (Roze, 1983; Jorge da Silva and Sites, 1999), we would add that the prefrontal does not contact the supralabials, and the first four infralabials contact the first pair of chinshields. The number of entire anterior subcaudals is variable in this species. The first ten are entire in NK 219 and the first 12 are entire in AMNH 120600, whereas all of the subcaudals are divided in FMNH 195899.

Distribution and Natural History.—Harvey (1998) identified NK 219 and reported this species for the first time from the Serranía de Huanchaca (Fig. 2); it was previously known only from the type locality. Roze (1983) observed that *Micrurus pyrrhocryptus* occurred on adjacent mountains and in the intervening lowlands. He suspected that *M. diana* might be restricted to the Serranía de Santiago. The Serranía de Santiago and the Serranía de Huanchaca are remnants of the Brazilian Shield and are ecologically very similar (Killeen and Schulenberg, 1998). Roze's (1983) characterization of the type locality as an "'island' surrounded by swampy lowlands" certainly applies to both localities during the rainy season.

Jorge da Silva and Sites (1999) report a personal communication from P. Bettella, who sent them a slide of a specimen taken from San Ramón (provincia Ñuflo de Chávez), Santa Cruz, Bolivia. We have not examined the slide and have not been unable to locate the specimen in the Museo Noel Kempff Mercado, where P. Bettella deposited most specimens he collected.

BOLIVIA. SANTA CRUZ. Velasco: Serranía de Huanchaca (NK 219). **Chiquitos:** "surroundings of Santiago, 700 m," (AMNH 120600, FMNH 195864, FMNH 195899, paratypes).

Micrurus hemprichii (Jan)

Elaps hemprichii Jan, 1858:523. COTYPES sex unknown, Colombia (MSNM, destroyed in World War II) and an unknown locality (NHMW, status unknown) [Schmidt (1953a) doubts that one of the types could have come from Colombia and proposes "vicinity of Bartica, British Guiana" as the new type locality. However, Roze (1955) argues that the original type locality may have been correct, and he reports a specimen from only a few kilometers of the Colombian border in Venezuela]. Boulenger, 1896:421; Boulenger, 1898a:131.

Micrurus hemprichii (Jan): Amaral, 1925:17; Amaral, 1930c:230; Amaral, 1948b:158; Hoogmoed, 1979:277; Fugler, 1986:57; Vanzolini, 1986:24; Fugler and Cabot, 1995:60.

Micrurus hemprichi hemprichi (Jan): Schmidt, 1953a:166; Golay et al., 1993:170.

Micrurus hemprichii hemprichii (Jan): Roze, 1955:481; Brongersma, 1967:73; Roze, 1970:210; Hoge and Romano, 1972:108; Hoge and Romano, 1973:125; Cunha and Nascimento, 1982:13; Nascimento et al., 1987:57; Campbell and Lamar, 1989:118; Jorge da Silva, 1993:71; David and Ineich, 1999:141.

Micrurus hemprichi ortonii Schmidt, 1953a:166. HOLOTYPE male, "Pebas, Peru" (MCZ 12423). Schmidt, 1955:348; Peters, 1960:530; Golay et al., 1993:170.

Micrurus hemprichii ortonii Schmidt: Roze, 1967:29; Roze, 1970:210; Hoge and Romano, 1972:108; Hoge and Romano, 1973:126; Carrillo de Espinoza, 1983:31; Dixon and Soini, 1986:142; Campbell and Lamar, 1989:118; David and Ineich, 1999:141.

Boulenger (1898a) reported on a single specimen of *Micrurus hemprichii* collected by Balzan from "Misiones Mosetenes" (presumably in the Serranía de Mosetenes, Cochabamba, Bolivia; Fig. 2). In his review of this species, the specimen was not examined by Schmidt (1953a), who pointed out that the record was

a “logical extension of the range along the Amazonian slopes of the Andes.” We did not examine the specimen and are aware of no new Bolivian material for this species. To our knowledge, morphological data have never been reported for the Bolivian specimen. Jorge da Silva (1993) described 30 specimens from Rondônia, near Bolivia’s northeastern border.

Micrurus lemniscatus (Linnaeus)

(Fig. 4)

Coluber lemniscatus Linnaeus 1758:224. HOLOTYPE “Asia” (in error, LECTOTYPE NRS L-93, designated by Roze, 1989) [Schmidt and Walker (1943) restricted the type locality to Belém, Pará, Brazil; however, Roze (1967) thought that the specimen most likely came from the northern Guianas].

Elaps lemniscatus (Linnaeus): Günther, 1859:85 (part); Cope, 1859:346; Günther, 1861:15; Jan, 1863:113a; Jan and Sordelli, 1872:42 table 5, figure 1; Cope, 1876:182; Boulenger 1896:430 (in part).

Elaps marcgravii (Wied-Neuwied): Boulenger, 1896:428 (part); Boulenger, 1898a:131; Werner, 1901:10.

Elaps frontifasciatus Werner, 1927:250. HOLOTYPE male, “Bolivia” (NHMW 18298).

Micrurus lemniscatus (Linnaeus): Beebe, 1919:216; Amaral, 1925:24; Amaral, 1926c:39 (in part); Schmidt 1936:201; Schmidt and Walker, 1943:294; Amaral, 1948a:9; Amaral, 1948b:158; Schmidt and Inger, 1951:464; Schmidt, 1955:349; Peters, 1960:531; Hoogmoed, 1979:277; Rivero-Blanco and Dixon, 1979:297; Fugler, 1986:57; Vanzolini, 1986:24; Nascimento et al., 1988:55; Fugler and Cabot, 1995:60; Di-Bernardo et al., 2001:60.

Micrurus helleri Schmidt and Schmidt, 1925:129. HOLOTYPE male, “Pozuzo, Huanuco, Peru” (FMNH 5577). [Added to synonymy by Amaral, 1930a:54]

Micrurus lemniscatus lemniscatus (Linnaeus): Amaral, 1944:89; Burger, 1955:40; Brongersma, 1967:73–74; Roze, 1967:32; Roze, 1970:212; Hoge and Romano, 1973; Roze, 1983:329; Cunha and Nascimento, 1982:15; Cunha et al., 1985:70; Campbell and Lamar, 1989:127; Golay et al., 1993:173; Roze, 1996:189.

Micrurus lemniscatus frontifasciatus (Werner): Roze 1967:34; Roze, 1970:212; Hoge and Romano, 1973:127.

Micrurus lemniscatus diutius Burger 1955:8. HOLOTYPE male, “Tunapuna, Trinidad” (FMNH 34472). Roze, 1955:483; Schmidt, 1957:62; Roze, 1967:34; Roze, 1970:212; Hoge and Romano, 1973:127; Roze, 1983:329; Campbell and Lamar, 1989:128; Golay et al., 1993:174; Roze, 1996:190; Kornacker, 1999:155.

Micrurus lemniscatus carvalhoi Roze, 1967:33, figure 11. HOLOTYPE male, “Catanduva, São Paulo, Brazil” (USNM 76341). Roze, 1970:212; Hoge and Romano, 1973:128; Roze, 1983:329; Campbell and Lamar, 1989:127; Roze, 1996:190.

Micrurus lemniscatus helleri (Schmidt and Schmidt): Roze, 1967:35; Hoge and Romano, 1973:128; Miyata, 1982:18; Roze, 1983:329; Carrillo de Espinoza, 1983:33; Dixon and Soini, 1986:143; Campbell and Lamar, 1989:128; Jorge da Silva, 1993:72; Golay et al., 1993:174; Carrillo de Espinoza and Icochea, 1995:19; Roze, 1996:191; Kornacker, 1999:156.

Micrurus frontifasciatus (Werner): Roze, 1983:313, 326. Campbell and Lamar, 1989:116 (in part); Golay et al., 1993:168; Roze, 1996:175 (in part); David and Ineich, 1999:140. [revised synonymy, see remarks]

Micrurus ibiboboca (Merrem): Fugler, 1986:57.

Diagnosis.—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad complete; (7) 2–6 red vertebrals separating first triad from parietals; (8) dorsal surface of head black with white band crossing snout; margins of scales within white band not edged in black; parietals partly red; (9) extent of black pigment in red and white rings variable; (10) white rings longest ventrally, never constricted or broken ventrally by black rings; (11) mental and some anterior infralabials entirely black (i.e., band across snout broken by entirely black infralabials) or red; (12) 9–15 triads on the body and 1–1.67 triads on the tail in Bolivian specimens (7–17 and 0.67–2 across the species range,

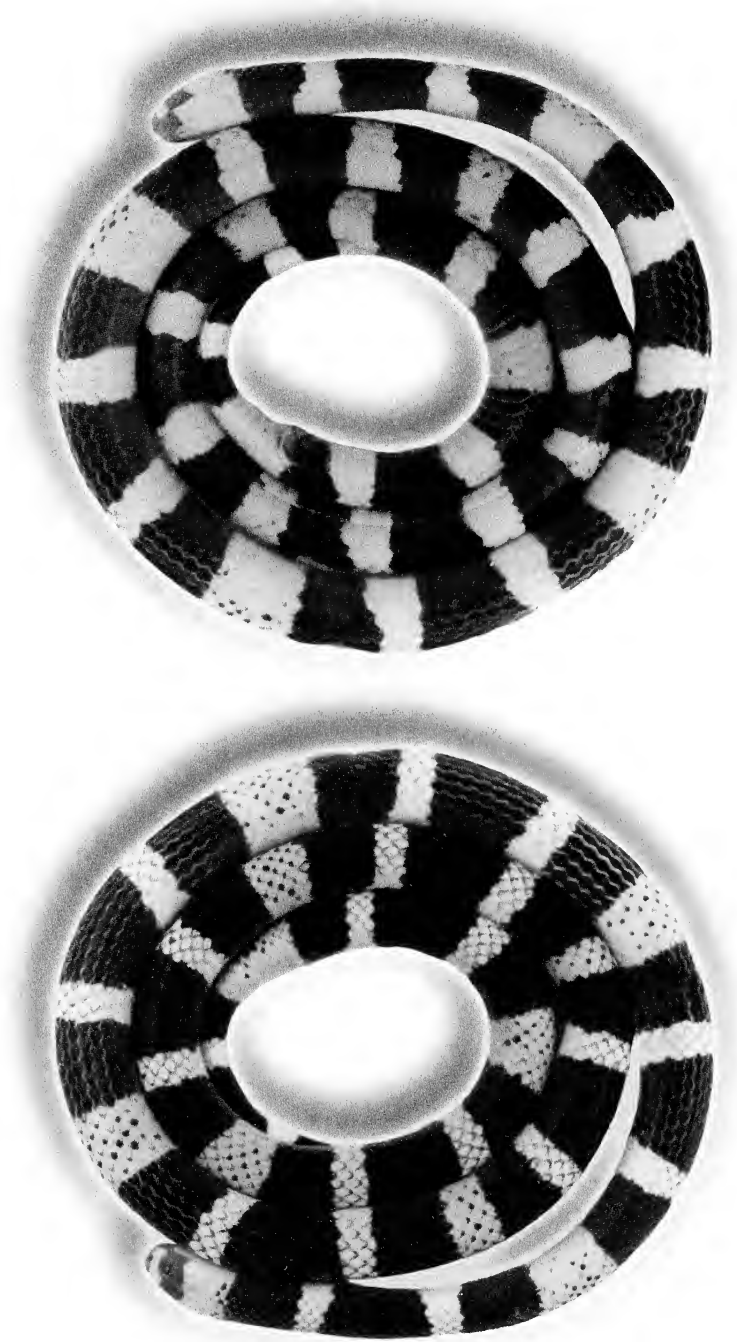


Fig. 4.—*Micrurus lemniscatus* (KU 183491 ♀, SVL 625 mm) from 21 km SW of Villa Tunari, Chapare, Cochabamba.

Campbell and Lamar, 1989); (13) white rings always smaller than exterior black rings in Bolivian specimens and elsewhere (Campbell and Lamar, 1989).

Description.—(based on 11 females, 8 males, and 6 unsexed juveniles). *Micrurus lemniscatus* is one of the most distinctive coralsnakes in Bolivia. Bolivian specimens were 244–1047 mm, the largest being a female (CBF 982). CBF 665 (also a female) with a snout-vent length of 995 mm would be the longest specimen, however most of its tail is missing. The tails of females were 6.6–10% (8.6 ± 1.0 , 9) and the tails of males were 8.0–11.3% (9.2 ± 1.2 , 7) as long as their snout-vent lengths. The length of the head accounts for 1.4–2.3% (1.9 ± 0.2 , 9) of snout-vent length in females and 2.0–2.4% (2.2 ± 1.4 , 7) in males. Eye-nostril distance is 21–24% (21 ± 1 , 5) of head length. The snout of this species is more bluntly rounded than is the snout of the superficially similar *M. pyrrhocyptus* and *M. serranus* (Fig. 6).

In our sample, variation in cephalic squamation is low. In one specimen (UMMZ 56891, 4.2%, 24), the prefrontal contacts the second supralabial on both sides. A single postocular is present on both sides of two specimens (8.3%, 24). In all but one specimen (95.8%, 24), 1+1/1+1 temporals are present. In UTA 34563, the sixth supralabial contacts the parietals on both sides (0+1/0+1 temporals). Only rarely (4.2% of the time, 24), the fourth infralabial fails to contact the first pair of chinshields. The mental does not contact the chinshields. Three to five (4 ± 1 , 25) gulars and preentrals separate the chinshields from 218–266 (239 ± 16 , 11) ventrals in females and 210–236 (220 ± 10 , 8) ventrals in males. Females have 27–38 (31 ± 3 , 11) and males have 29–39 (33 ± 4 , 8) subcaudals. The anal and the subcaudals are divided in most specimens. In three individuals (12.5%, 24), the first four or five subcaudals are entire.

This species is characterized by four well-defined bands (black, white, black, red) on the dorsal surface of the head. The first black band overlaps the rostral, internasals, prenasal, and first infralabial. The scales in the white band are immaculate and do not have black margins. The white band overlaps the prefrontals, the anterior edge of the frontal, and most of the postnasal, preocular, and supralabials 2–3. In one specimen (CBF 665), the white band does not reach the supralabials, the first five of which are uniformly black. The extent of the bands is somewhat variable so that the anterior one-fourth of the supraoculars may also be white in some specimens. The second and broader black band covers most of the frontal and the anterior one-third of the parietals, supraoculars, postoculars, supralabials 4–5 and part of the anterior temporals. In some specimens, the anterior edge of the sixth supralabial is also covered by this band. The parietals may be immaculate, have black apices (e.g., UMMZ 56891), or have irregular black edges and smudges (e.g., NK 968, UMMZ 67928). AMNH 110449 is unusual in having immaculate black prefrontals that restrict the white band to the sides of the head (USNM 19726 from Loreto, Peru, exhibits a similar pattern).

Banding on the head is interrupted by a distinctive chin pattern. In most specimens, the mental and first three infralabials are immaculate black and sharply contrast with the mostly white chinshields. This black infralabial pattern interrupts the white prefrontal band on the sides of the head (Fig. 6). In some specimens, the black infralabials are present on one side only (e.g., CBF 442 and 458) or absent altogether (e.g., UMMZ 57696, small black blotch present on one side; USNM 193722–23 from Huanuco, Peru, also lack black infralabials). The gulars and preentrals are usually immaculate.

Bolivian specimens of *Micrurus lemniscatus* have 9–15 (10 ± 1 , 24) triads on

the body and one to one and two-thirds on the tail. The first triad is separated from the parietals by 2–5.5 (3.0 ± 0.9 , 23) red vertebral scales. The amount of black pigment in the red and white rings is highly variable in our sample, and we find no evidence that increased melanism is correlated with ontogeny. Some of the largest specimens (e.g., UMMZ 57696, 942 mm long; CBF 426, 749 mm) have nearly immaculate white rings, whereas several juveniles (e.g., UTA 34563, 300 mm long) have scales with black apices in nearly all of the white rings. In most specimens all of the rings on the body are complete. In UMMZ 56891, the exterior rings are broken on the flanks in triads 7–9: i.e., complete middle rings are flanked by black dorsal and ventral blotches in these triads. Ventrally, the black rings do not interrupt the white rings and the rings are almost always immaculate. In Bolivian specimens, the exterior black rings are smaller than or equal to the middle black ring (57–100%, 77 ± 13 , 23), and the white rings are always smaller than the exterior black rings (20–71%, 48 ± 16 , 23). In the median triad, the middle black ring was 50–233% (132 ± 50 , 23) as long as the red ring.

In life (field notes of M. B. Harvey based on MBH 6129), the white band across the snout and white rings of the first two triads had a faint yellow tinge; the remaining white rings were grayish white. The red rings were Flame Scarlet (#15, Smithe, 1975).

Natural History.—NK 564 was found eating a swamp eel (*Synbranchus* sp.). The specimen from El Refugio was caught in August in a small mammal trap set next to a rapidly drying grassy pond in savanna, approximately 0.5 km from forest. When disturbed, the specimen hid its head under its coils, elevated its tail, and waved the underside of its tail at the observer. In addition to *Synbranchus*, this species also feeds on amphisbaenians, caecilians, small teiids, and other fish (Roze, 1983; Vanzolini, 1986). Beebe (1946) also collected this species in marshy fields adjacent to forest.

Distribution and Comparative Material.—In Bolivia (Fig. 5), the range of this species is more extensive than that depicted by maps published by Campbell and Lamar (1989) and Roze (1996). As for many other Amazonian species, *Micrurus lemniscatus* occurs in the humid forests of the Andean foothills as far south as Santa Cruz. The discovery of this species in the Serranía de Santiago is, at first, surprising because most of the herpetofauna in this area is Chacoan (Gans, 1960). However, stands of high tropical dry forest separate the Beni from the lower scrub-like vegetation of the Gran Chaco. The Serranía de Santiago lies in this band as does Finca Dos Milanos, and the region is inhabited by both Amazonian (e.g., *Apostolepis nigroterminata*, Harvey, 1999) and Chacoan reptiles and amphibians.

BOLIVIA. BENI. Cercado: El Toco, 14°53'06"S, 64°39'03"W (NK 968). Gral. José Ballivián: San Borja (CBF 458), Rurrenabaque (NK 1938). Marban: 60 km S Trinidad (NK 564). Marmoré: San Joaquín (FMNH 152316). Yacuma: Estancia "Totai" = Toataisal (NK 1958), Estancia Kamandu, 57 km E San Borja (CBF 426), Espíritu (CBF 441–42, CBF 456). Unknown: "Rio Itenez, Puerto Capitan Vazquez," not traced (AMNH 110449–50), "Villa Bella Rio Beni," not traced (UMMZ 57696), "along Beni River" (AMNH 22272), no other data (AMNH 2977, CBF 1450). **COCHA-BAMBA.** Chapare: 21 km SW Villa Tunari, 680 m (KU 183491). **LA PAZ.** Larecaja: Zona Unutluni, 2 km del Río Tora, 250 m [southwest] del Guanay, 1200 m, (CBF 515). **Sud Yungas:** Sapecho, (CBF 1170). **PANDO.** Frederico Román: "Manao" = Nuevo Manao, "extreme NE corner Bolivia junction of Rio Abuna with Madeira" (UMMZ 56891). **Manuripi/Madre de Dios (border):** Junction of the Río Madre de Dios and Río Sena, bank not specified (UMMZ 59772). **SANTA CRUZ.** Andrés Ibáñez: Km 14 on old road to Cochabamba (NK 513). **Chiquitos:** Finca Dos Milanos (UTA 34563), Campamento Murcielago, 59° 03 S, 18° 06' W (NK 2247). **Ichilo:** Buena Vista (UMMZ 67928), San Carlos (NK 104), Campamento Espejo, Río Blanco, Parque Nacional Amboró (NK 2027). **Ñuflo de Chávez:** Las Trancas (NK 2028), Concepción (CBF 665). **Velasco:** Estancia El Refugio (uncatalogued, collector's tag M. B. Harvey 6129).

ECUADOR. MORONA-SANTIAGO: USNM 283970–71. **PASTAZA:** USNM 232437–41.

PERU. HUANUCO: USNM 193720–23. **LORETO:** USNM 197295–96.

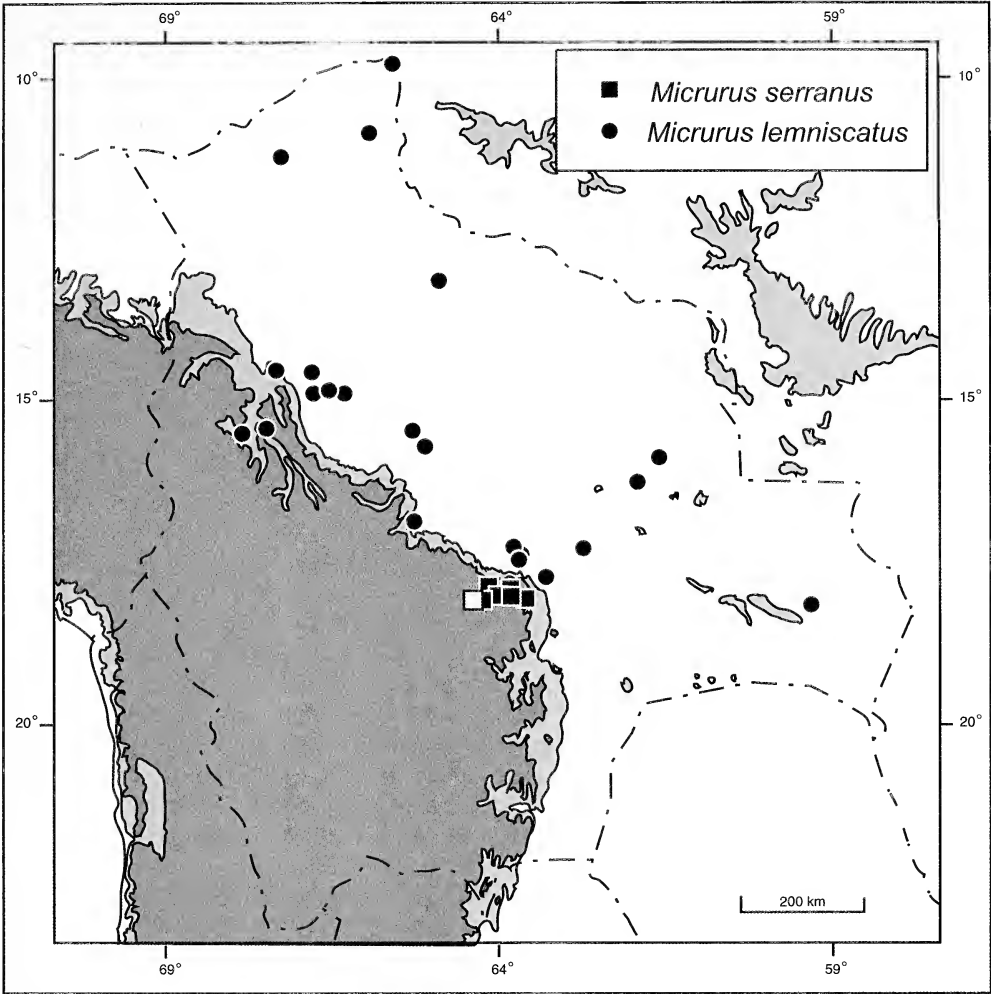


Fig. 5.—Distribution of *Micrurus lemniscatus* and *M. serranus*.

SURINAME. SURINAME: USNM 13823
TRINIDAD. ST. GEORGE: USNM 286963.

Remarks.—Werner (1927, page 250) described an adult male coralsnake (NHMW 18298) collected by Staudinger from “Bolivia” as *Elaps frontifasciatus*. The original description is inadequate to unequivocally identify this species. However, Heinz Grillisch of the NHMW kindly examined the specimen and answered several of our questions regarding its characteristics. From Werner’s description, the holotype had a snout-vent length of 1040 mm and tail length of 75 mm. It has 1+1 temporals, 222 ventrals, a divided anal plate, and 31 divided subcaudals. The snout is black and a long black band crosses the ocular region to cover supralabials 3–5. The suture between the parietals bears a large black spot. The body has eight triads with one complete and one incomplete triad on the tail. In each triad, the middle black rings (about 8 scales long) are longer than the external ones (about 5 scales long). Finally, the white rings are as long as the external

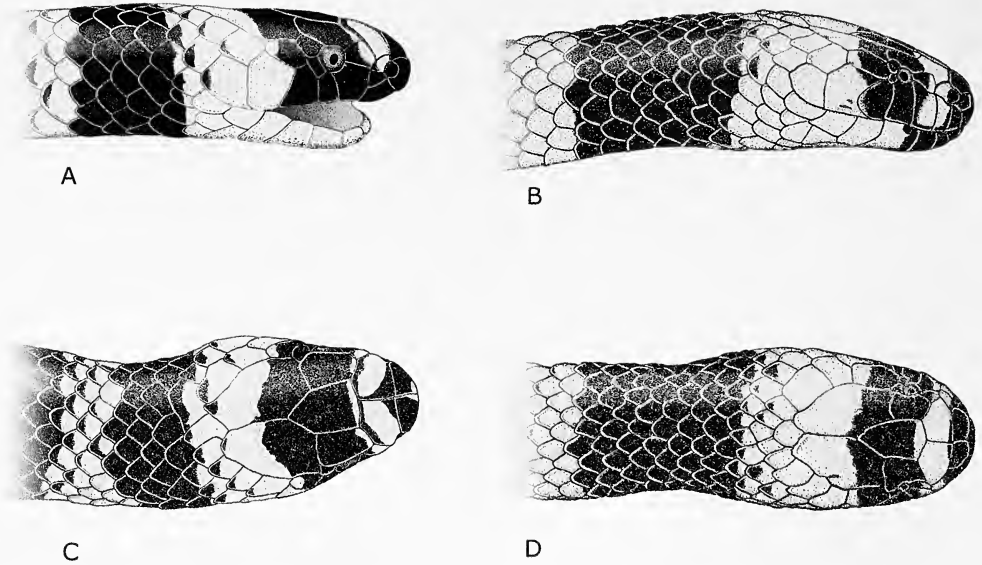


Fig. 6.—Cephalic squamation and pattern of *Micrurus serranus* (A, C, Holotype, UTA 34561 M) and *M. lemniscatus* (B, D, KU 183491).

black rings. Dr. Grillitsch further clarified that white rings are longest ventrally and all rings are immaculate ventrally. The white band across the snout encompasses part of supralabial 1 and 3 and all of 2, the preocular, the prefrontals, and the anterior edge of the frontal and supraoculars. Importantly, the scales in the white band are not edged in black. The ventral surface of the head is immaculate to the level of the first body triad.

Werner's species was correctly thought to be synonymous with *Micrurus lemniscatus* by Amaral (1930a). However, later authors (Campbell and Lamar, 1989; Roze, 1996) thought it was conspecific with the undescribed species (Fig. 6) we name below and known to these authors from photos from Cochabamba (Campbell and Lamar, 1989, their figure 55) and an unknown locality in Bolivia (Roze, 1996, his color figure 28). Unlike the holotype of *M. frontifasciatus* and other *M. lemniscatus* (characteristics of *M. lemniscatus* in parentheses), the scales in the prefrontal band have black edges (scales in band uniformly white), the white rings are invaded by the black rings ventrally and have prominent black blotches (white rings immaculate ventrally), and the white rings are longest dorsally and shortest ventrally (the reverse is true) in *M. serranus*. In most specimens of *M. lemniscatus* uniformly black anterior infralabials interrupt the white prefrontal band (never the case in *M. serranus*), however, like the holotype of *M. frontifasciatus*, occasional specimens of *M. lemniscatus* have immaculate chins on one (e.g., CBF 458) or both (e.g., NK 513) sides.

We were unsuccessful in our attempts to determine a more precise locality for Werner's holotype. Mr. Staudinger was an insect dealer in Dresden, Germany. Entomologists at the Zoologisches Museum in Berlin where Staudinger's nearctic butterfly collection is housed were unable to confirm that Staudinger had visited Bolivia. Roze (1996) reported this species from "low and high mountain dry forest, cloud forest and lowland gallery forest on the eastern slopes of the Andes

in southeastern Peru and northern Bolivia, between about 600 and 2500 m.” Presumably, Roze thought the holotype came from low elevations in the Yungas of La Paz and believed it to occur at higher elevations in dry intermontane valleys based on communications with Noel Kempff Mercado, who supplied Roze’s color figure 28 of *Micrurus serranus*. Roze’s concept of this species is a composite of *M. lemniscatus* and *M. serranus*. The distribution he (Roze, 1996) reports for *M. frontifasciatus* is not applicable to any species of coralsnake.

Micrurus frontifasciatus was recently reported from Almeirim, Pará, Brazil (Guedes, 2000). This locality on the north bank of the Amazon and near the river’s mouth is 1600 airline km from the known range of the exclusively montane species *M. serranus*. Not having examined the specimen, we prefer not to speculate as to its identity.

Concerns about the reality of subspecies of *M. lemniscatus* have been registered (Cunha and Nascimento, 1982; Abuys, 1987; Nascimento et al., 1988). The subspecies are defined by number of ventrals, number of body triads, and length of the white rings. When a recent key to the subspecies (Roze, 1996) was used to identify our sample, 21% of the sample keyed out to *M. l. carvalhoi* (white rings 1–1.5 dorsals long), 53% keyed out to *M. l. diutius* (ventrals fewer than 225 in males and fewer than 242 in females), and 26% keyed out to *M. l. helleri* (ventrals more than 228 in males and more than 242 in females). However, each of the specimens that keyed to *M. l. carvalhoi* has fewer than 225 ventrals if a male and fewer than 242 if a female. Thus, these specimens would be classified as *M. l. diutius* because male *M. l. carvalhoi* have 228–254 ventrals and females have 250–263 ventrals (Roze, 1996). Although most Bolivian specimens of *M. lemniscatus* key to *M. l. diutius*, this subspecies is thought to occur in northern South America not extending south of the Amazon. Bolivia is not included in published ranges of *M. l. diutius* (Campbell and Lamar, 1989; Roze, 1996). The race of *M. lemniscatus* in Bolivia has previously been referred to *M. l. helleri*. We do not believe that these observations suggest an allopatric population or wider range of *M. l. diutius*. The characters used to define these subspecies are unreliable, and the subspecies themselves may not be valid. Nonetheless, some populations currently referred to *M. lemniscatus* represent distinct evolutionary lineages (Jorge da Silva and Sites, 2001). It remains to be seen whether more careful revision of this complex will support the subspecific taxa, and their use should be abandoned in the meantime.

Micrurus narduccii narduccii (Jan)

(Fig. 7)

Elaps narduccii Jan, 1863b:222. HOLOTYPE lost, “Bolivia” (CSI, number unknown; type locality restricted to “Buenavista, Provincia de Santa Cruz” = Buena Vista, Provincia Ichilo, by Roze and Bernal-Carlo, 1987). Boulenger, 1896:433; Griffin, 1916:220.

Micrurus narduccii (Jan): Schmidt, 1936:190 (in part); Romano, 1972:113 (in part); Campbell and Lamar, 1989:134 (in part).

Leptomicrurus narducci (Jan): Roze, 1967:3; Hoge and Romano, 1973:128 (in part).

Leptomicrurus narduccii (Jan): Schmidt, 1937:363 (in part); Hoge and Romano, 1966:5; Fugler and Cabot, 1995:60.

Micrurus narducci (Jan): Fugler, 1986:57.

Leptomicrurus narduccii narduccii (Jan): Roze and Bernal-Carlo, 1987:591; Roze, 1996:134.

Micrurus narduccii narduccii (Jan): David and Ineich, 1999:147.

Diagnosis.—(1) Dorsum black except for orange nuchal ring and, often, an orange ring around base of tail; circular orange or yellow spots on venter; (2)

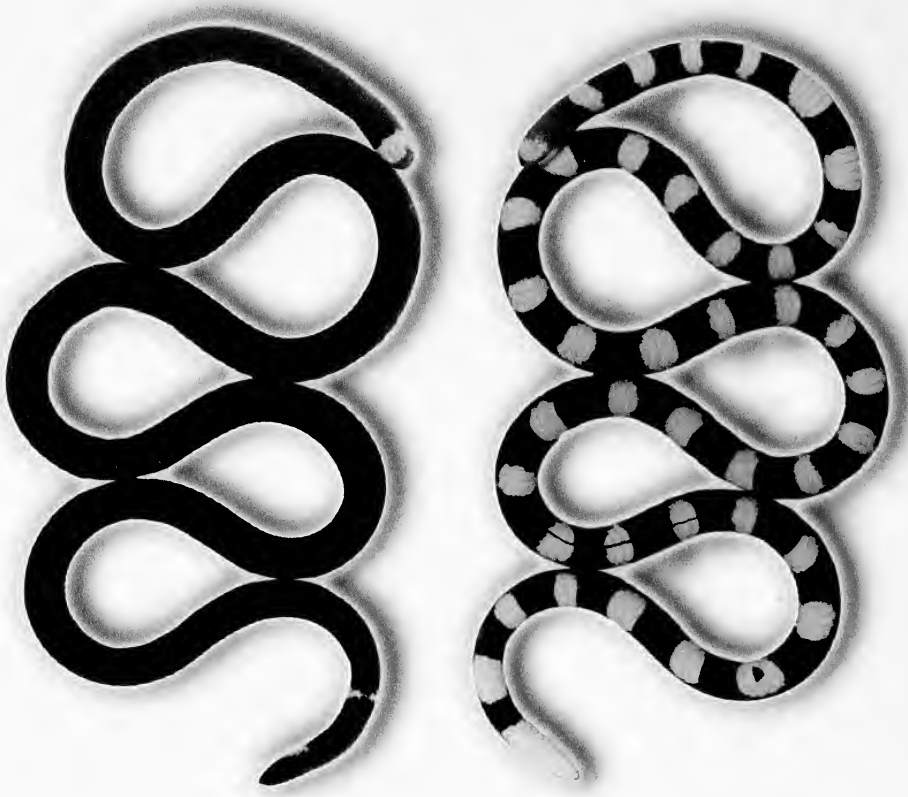


Fig. 7.—*Micrurus narduccii narduccii* (UMMZ 67891 M, SVL 462 mm) from Buena Vista, Andrés Ibáñez, Santa Cruz.

hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental broadly contacting chinshields; (5) anal scale usually divided; (6) dorsal head scales immaculate black except for orange band crossing all of frontal and anterior portions of parietals to supralabials and onto underside of head; (7) subcaudals 17–20 in females and 23–26 in males.

Description.—(based on 10 females and 12 males). *Micrurus narduccii* is not only the most distinctive of Bolivia's coralsnakes, but also its most sexually dimorphic. The sexes are immediately recognizable on the basis of nonoverlapping ventral counts, subcaudal counts, and relative tail and snout-vent lengths. In our sample, females were 421–579 mm in total length, and their tails were 3.6–4.5% (4.1 ± 0.3 , 9) as long as their snout-vent lengths. Males were 406–528 mm long, and their tails were 5.8–7.1% (6.7 ± 0.4 , 12) as long as their snout-vent lengths. Relative to congeners, the body of this species is much more attenuate so that head length accounts for only 1.3–1.5% (1.4 ± 0.1 , 8) of snout-vent length in females and 1.5–1.7 (1.6 ± 0.1 , 11) in males. The diameter of the eye is comparable to other coralsnakes and is 9–14% (12 ± 1 , 15) of head-length; eye-nostril distance is 20–24% (22 ± 1 , 15) of head-length.

Bolivian *Micrurus narduccii* have the cephalic squamation characteristics typ-

ical of most congeners. The prefrontals do not contact the supralabials in any of our sample. Two postoculars are invariably present and usually followed by 1+1/1+1 temporals. Two specimens have 1+2 temporals on one side only, and one specimen lacks the first temporal (i.e., 0+1) on one side. The supraoculars are 67–87% (78 ± 7 , 15) as wide as the frontal. Supralabials 4 and 5 are partially fused leaving a subocular on one side and are completely fused on the other side of UMMZ 63169. All other specimens have 7/7 supralabials. The mental broadly contacts the chinshields in all specimens. The first three (20% of the time, 22) or four (80%, 22) infralabials contact the first pair of chinshields, and the fourth or third and fourth contact the second pair. Four (77%, 22) or five (23%, 22) gulars and preventrals separate the chinshields from the ventrals. Females have 314–324 (318 ± 3 , 10) ventrals and 17–20 (18 ± 1 , 9) subcaudals, whereas males have 264–278 (274 ± 5 , 12) ventrals and 23–26 (25 ± 1 , 12) subcaudals. The anal plate and all subcaudals are divided.

The black snout and orange frontoparietal band are immaculate. The extent of the frontoparietal band varies somewhat: the frontal, postoculars, first temporals, and supralabials 5 and 6 are completely orange. The band covers two-thirds to three-fourths of the parietals, part of the second temporals, and most or all of the supraoculars. In some specimens the band may also overlap the posterior edge of the prefrontals, posterior edge of supralabial 3, all of 4 and the anterior edge of supralabial 7. Thus, the eye is ordinarily enclosed in the black band covering the snout, the only exception being UMMZ 67893, where the preocular and supralabial 3 are also yellow on one side only. On the ventral surface of the head, infralabials 6 and 7 and sometimes part of 5, the gulars, and the first few ventrals are black. The rest of the chin is orange.

The dorsum is immaculate black. Ventral blotches are orange (pale yellow in preservative), extend onto the paraventrals, and cover from 1.5–6 ventrals. On individual specimens, size of blotches is not constant. However, the different-sized blotches and spacing of the blotches do not seem to form any consistent pattern that might be interpreted as being derived from the triad pattern. In some specimens (e.g., UMMZ 60566), several pairs of ventral blotches are fused leaving a black spot or one black ventral in the center of each fused pair. With longer bodies, females have more blotches (44–52; 47 ± 3 , 10) than males (38–44; 41 ± 2 , 12).

Male specimens have 2–3 blotches on the ventral surface of the tail. Except for the first subcaudal, the ventral surface of the tail is uniformly yellow in most (67%, 10) females or two discrete blotches may be present (33%, 10). A usually complete (incomplete in UMMZ 63168) ring encircles the tail at the level of the third subcaudal in both sexes, and a second ring in the middle of the tail is broken vertebally.

Natural History Notes.—Two Bolivian specimens (UMMZ 60565 and 67893) had swallowed whole *Bachia dorbignyi* head first. A third specimen (UMMZ 60568) contained a tail which appears to be from *B. dorbignyi*. The distal tip of this tail was swallowed first.

Distribution.—**BOLIVIA. SANTA CRUZ.** Andrés Ibáñez: Santa Cruz de la Sierra (CM 114), Espejillos (NK 489), Terevinto (NK 517), El Potrerillo (NK 2029), Buena Vista [CM 2705, 2870, 2895, MCZ 19724, UMMZ 60565–60568, UMMZ 63168, UMMZ 67891 ($n = 3$), UMMZ 67892, UMMZ 67893]; Río Surutú (UMMZ 63169–63170). **Sara:** unknown (CM 8).

Remarks.—Most references to this species are based partially or exclusively

(the latter publications purposefully left out of our synonymy) on specimens of *Micrurus narduccii melanotus* (Peters). The account by Campbell and Lamar (1989) also includes data for *Micrurus scutiventris* Cope. These authors considered *Micrurus karlschmidti* Romano (replacement name for *Leptomicrurus schmidti* Hoge and Romano and a synonym of *M. scutiventris*) to be a synonym of *M. narduccii*. The subspecies of *Micrurus narduccii* appear to be allopatric, and numbers of subcaudals do not overlap between females and rarely overlap between males of the two subspecies. Our ranges for subcaudals (17–20 in females and 23–26 in males) are slightly broader than those reported by Roze (1996); female *M. n. melanotus* have 21–27 subcaudals and males have more than 24–35 (usually 28–35 based on 30 specimens, Roze, 1996). Campbell and Lamar's (1989) map does not include the range of *M. n. narduccii*, the shaded portion in the Pando region is probably based on the imprecise type locality "Bolivia." *Micrurus narduccii narduccii* is known only from the rainforests at the base of the Andes around Santa Cruz de la Sierra (Fig. 2), and recent collecting efforts elsewhere in the country have failed to discover additional populations.

Micrurus obscurus (Jan), **new combination**

(Fig. 8A, 8C)

Elaps corallinus var. *obscura* Jan in Jan and Sordelli, 1872:41, plate 6, figure 2. HOLOTYPE (MSNM, destroyed in World War II), "Lima" in error [type locality designated as "Iquitos, Peru" by Schmidt, 1953b:175].

Elaps heterozonus Peters, 1881:52. HOLOTYPE from "Sarayacu (Ecuador)" (ZMB 9813). Boulenger, 1896:417; Barbour and Noble, 1920:619; Amaral, 1925:18.

Elaps spixi (Wagler): Werner, 1901:10.

Elaps princeps Boulenger, 1905:456. SYNTYPES "Province Sara, Department Santa Cruz de la Sierra, Bolivia" (Roze, 1989:14, designated BMNH 1946.1.20.44, a male, as a lectotype). Griffin, 1916:220. [new synonymy, see remarks]

Micrurus spixii (Wagler): Schmidt, 1936:198 (in part); Amaral, 1948a:159; Vanzolini, 1986:24; Fugler, 1986:58 (in part); Fugler and Cabot, 1995:60 (in part).

Micrurus spixii obscurus (Jan): Schmidt and Walker, 1943:294.

Micrurus spixi obscurus (Jan): Schmidt, 1953b:175; Schmidt, 1955:350; Roze, 1955:476; Peters, 1960:532; Lancini, 1979:192; Golay et al., 1993:181.

Micrurus spixi princeps (Boulenger): Schmidt, 1953b:175; Golay et al., 1993:182.

Micrurus spixii princeps (Jan): Roze, 1967:42; Roze, 1970:218; Hoge and Romano, 1973:129; Duellman, 1978:261; Miyata, 1982:18; Carrillo de Espinoza, 1983:43; Roze, 1983:335; Dixon and Soini, 1986:146; Campbell and Lamar, 1989:146; Carrillo de Espinoza and Icochea, 1995:19; Roze, 1996:216; Kornacker, 1999:159.

Micrurus spixii princeps (Boulenger): Roze, 1967:43; Roze, 1970:218; Roze, 1983:335; Campbell and Lamar, 1989:146; Roze, 1996:217.

Diagnosis.—(1) Dorsal pattern of yellow, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually divided; (6) first triad usually incomplete (if complete, the first black ring is very short and edges the parietals; a "remnant" of this ring is often evident as a row of black scales on the side of the neck); two black rings on neck, the first strongly angled anteriorly along midline; (7) dorsal surface of snout red, parietal region yellow; black band crossing frontal and supraoculars to supralabials; (8) apices of yellow rings with more black pigment than apices of scales in red rings; (9) yellow rings longest ventrally, some black rings greatly constricted or interrupted ventrally; (10) mental and some anterior infralabials edged in black, remaining scales of chin mostly immaculate; (11) parietals immaculate yellow or with black blotching; scales of snout moderately blotched; (12) pre-

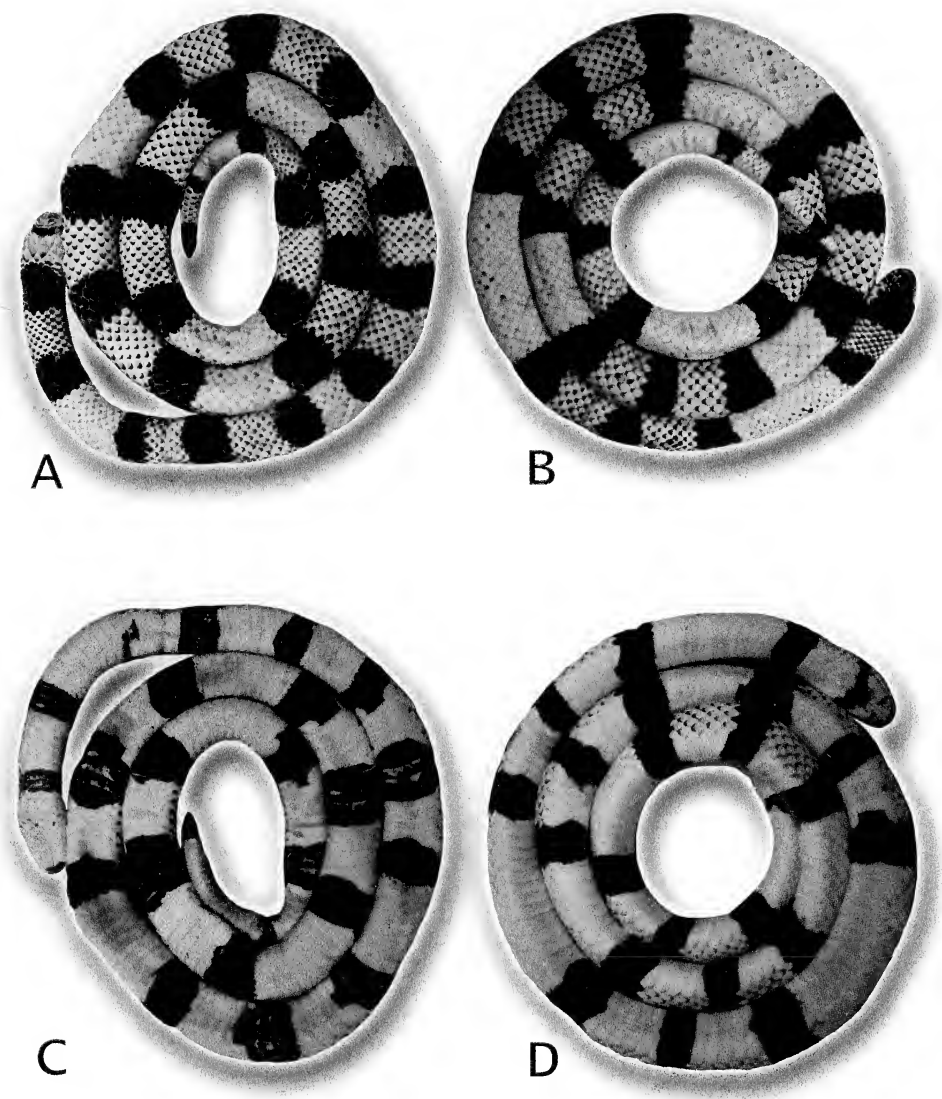


Fig. 8.—*Micrurus obscurus* (A, C; NK 158 F, SVL 1124 mm) from Parque Nacional Amboró, Ichilo, Santa Cruz, and *M. spixii* (B, D; NK 604 M, SVL 1172 mm) from the Serranía de Huanchaca, Velasco, Santa Cruz.

frontal contacting the supralabials in about 60% of the specimens; (13) 6–9 body triads (as few as 4 in specimens outside Bolivia, Roze, 1996), 0.67–1 triads on tail; (14) yellow rings longer or only slightly shorter than exterior black rings.

Description.—(Based on 12 males, 11 females, and 7 unsexed juveniles). This species is the largest Bolivian coralsnake. Extremes in our sample are 1345 mm (CM 126) and 1186 mm (NK 158) for the largest male and female, respectively,

and 278 mm for the smallest juvenile (AMNH 122498). The tail is 5.1–6.2% (5.8 ± 0.4 , 10) as long as snout-vent length in females and 5.0–7.0 (5.7 ± 0.5 , 12) as long in males. Head length accounts for 2.0–3.3% (2.4 ± 0.4 , 9) of snout-vent length in females and 2.0–2.5 (2.4 ± 0.3 , 12) in males. The distance from the anterior border of the eye to the center of the nostril accounts for 14–22% (20 ± 2 , 21) of head length.

Contact between the prefrontals and the supralabials is common in this species, occurring 60% (30) of the time. In our sample, 7/7 supralabials and 2/2 postoculars are always present; the third and fourth supralabials invariably enter the orbit. Temporals usually (67% of the time, 31) number 1+1/1+1; although about one-third of the specimens have 1+2 temporals on one or both sides (33%, 31). The supraoculars are 64–92% (73 ± 8 , 22) as wide as the frontal.

Seven infralabials are invariably present and the first pair always separate the mental from the chinshields. The first three (22%, 30) or the first four (78% of the time, 30) infralabials contact the first pair of chinshields so that the third and fourth or just the fourth contact the second pair. Four to eight (5 ± 1 , 27) gulars and preentrals separate the chinshields from 216–222 (218 ± 3 , 10) ventrals and 18–22 (21 ± 1 , 10) subcaudals in females and 211–220 (216 ± 3 , 12) ventrals and 20–23 (21 ± 1 , 12) subcaudals in males. Some entire subcaudals are invariably present on the proximal one-third of the tail and number from 2–8 (4 ± 1 , 26).

The rostral, nasals, internasals, and prefrontals have black blotches and edging. A subrectangular black blotch lies in each prefrontal. A well-defined black interorbital band is angled anterolaterally across the eye and onto supralabial 3 and the upper edge of (4). It overlaps about one-half to three-fourths of the supraoculars and frontal. The parietals may be immaculate (e.g., CM 126, 2828) or have black apices (e.g., CM 2841, 2952) in specimens from Santa Cruz. A specimen from Pando (NK 259) closely resembles upper Amazonian specimens of *Micrurus obscurus* in being more melanic overall and in having a single large blotch in the center of each parietal. Each parietal is almost one-half black because of greatly enlarged black apices in UMMZ 60733 from Buena Vista, SC. The mental is mostly to completely black and, frequently, the first one or two infralabials have black edges. The rest of the gular region is nearly to completely immaculate.

There are 6–9 (7 ± 1 , 31) triads on the body and usually (93%, 31) two-thirds of a triad on the tail. Two specimens (MCZ 24895, UMMZ 60777, 7%, 31) have a complete triad on the tail. The first triad is two-thirds and the first black ring is a middle ring. “Remnants” of the “missing ring” are seen as a row of prominent black apices in a line just behind the rictus and crossing the first vertebral. In Bolivian specimens, a black gular band is usually absent, however some of the lateral gular scales may have black apices, and a poorly defined gular band 2 scales long at midventer is present in NK 259 and CBF 1011. The first black ring on the neck strongly projects anteriorly for 5–11 (7 ± 1 , 23) vertebrae and shortens ventrally to 1–3 ventrals. It is separated from the parietals by 0–3.5 (1.4 ± 0.6 , 30) yellow vertebrae. In CBF 1011, the first black ring is particularly long and reaches the parietals. The second ring is only somewhat shorter to almost one-half as long ventrally. Elsewhere on the body and tail, black rings are consistently longest vertebrally and constricted on the flanks. Midventrally, the first and last black rings of some triads project into the center of the first and last yellow ventral. A few (1–7) black rings are incomplete ventrally. In most specimens, the last black ring in front of the cloaca is incomplete or altogether absent.

The red rings bear some diffuse speckling or some faint, black apical tips. In the specimen from Pando, all except the first two rows of dorsals bear black apical tips. However, the amount of black in the red scales of this specimen is only about one-third as much as in the yellow scales. The yellow scales have heavy black apices in all specimens.

Micrurus obscurus is often characterized as having yellow rings longer than the black rings. However, the exterior black rings are one-half to one vertebral longer than the yellow rings in seven specimens; both the exterior and middle black rings are longer than the yellow rings in FMNH 35733. At midbody, the red rings are 6–11.5 (8 ± 2 , 28), the exterior black rings 3–6 (4 ± 1 , 28), the yellow rings 3.5–7.5 (5 ± 1 , 28), and the middle black ring 3–5 (4 ± 0.5 , 28) vertebrae long. The middle black rings are 35–75% (54 ± 1 , 28) as long as the red rings. The exterior black rings are 67–125% (105 ± 21 , 28) and the yellow rings are 80–187% (119 ± 24 , 28) as long as the middle black ring.

Distribution and Comparative Material.—*Micrurus obscurus* occurs in the upper Amazon basin from Colombia and Southern Venezuela to the vicinity of Santa Cruz de la Sierra (Fig. 9).

BOLIVIA. BENI. Gral. José Ballivián: Rurrenabaque (AMNH 22498). Moxos: Oromomo (CBF 1011). Vaca Díez: Riberalta (NK 512). PANDO. Nicolás Suárez: San Carlos (NK 259). SANTA CRUZ. Andrés Ibáñez: Santa Cruz de la Sierra (CM 126), Terevinto (NK 483). Ichilo: Río Saguayo, Parque Nacional Amboró (NK 158), Río Surutú (UMMZ 63818–63819), “Río Pitasama a 14 km desde el Río Surutú,” Parque Nacional Amboró (NK 440), Buena Vista [AMNH 35985, CM 2763, MCZ 24895, FMNH 35729, FMNH 35731, FMNH 35733, UMMZ 60733, UMMZ 60776–60777, UMMZ 60779, UMMZ 60781, UMMZ 63816 ($n = 2$), UMMZ 63818, UMMZ 67929–67930], Río Surutú, W of Buena Vista (CM 2841), Río Colorado (CM 2952), unknown (CM 2961). UNKNOWN: CM 2828, NK 2023–24.

ECUADOR. MORONA-SANTIAGO: USNM 232481. NAPO: USNM 232482–83. PASTAZA: USNM 232491–93, USNM 287947–50. UNKNOWN: FML 1693.

PERU: HUANUCO: USNM 193724–29.

Remarks.—Eastern Bolivia may be the only location where species of the *Micrurus spixii* complex are in sympatry (Fig. 9). If the status of these taxa is to be established, conclusions will necessarily have to be based on the samples from Bolivia.

Three characters have been used to distinguish the subspecies of *Micrurus spixii*: number of body triads and length and position of the black nuchal ring. Among specimens we examined, there is more overlap in the first two of these characters than Schmidt's (1953b) and Roze's (1996) keys and accounts would lead one to believe. The nuchal ring extends for eight or more (up to 11) vertebrae in fifty percent of the specimens from the vicinity of the type locality of *M. s. princeps* (Santa Cruz de la Sierra), so that these specimens key out to *M. s. obscurus* in Roze's key. Roze (1996, his couplet 1, p. 215) characterizes the nuchal ring of *obscurus* as extending for 8 or more dorsals and that of *princeps* as extending for seven or fewer. Schmidt (1953b) used number of body triads to separate *M. s. obscurus* and *M. s. princeps*. However, as Schmidt's data (top of his page 178) indicate, overlap among these putative subspecies is considerable: 29% of the *M. s. obscurus* he examined had 6–7 body triads, the most common (90% of Schmidt's specimens) condition in *M. s. princeps*. *Micrurus s. martiusi* and *M. s. spixii* have the nuchal ring covering the parietals and are separated by Roze (1996) and Schmidt (1953b) on the basis of numbers of body triads. Again these ranges overlap. In Roze's key, *M. s. martiusi* is characterized as having six to eight complete triads on the body, *M. s. spixii* as having four to six complete triads. Interestingly, although Schmidt (1953b) and Roze (1996) assigned Bolivian

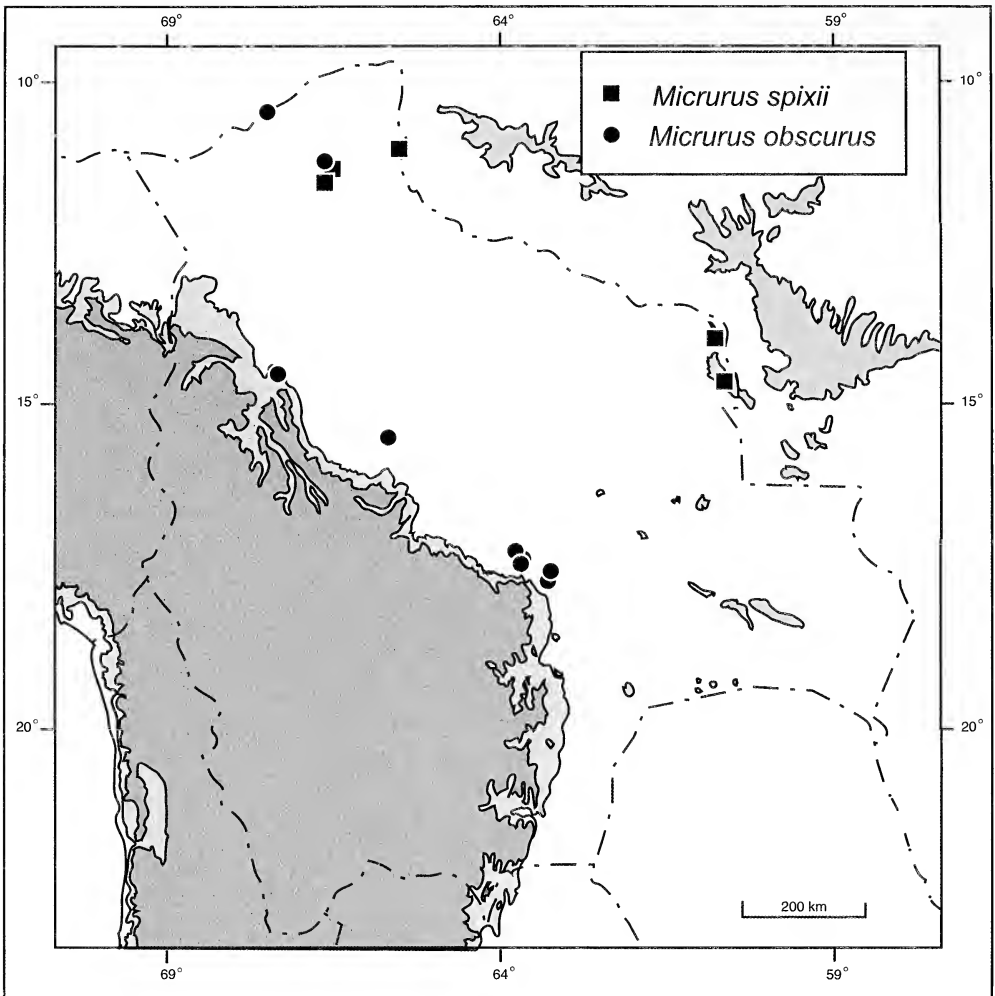


Fig. 9.—Distribution of the *Micrurus spixii* complex in Bolivia.

specimens to *M. s. spixii*, all but one (AMNH 22277) of the specimens we examined had seven or more body triads, thus keying out to *M. s. martiusi*. Roze's (1996) map provides dot localities for four specimens which he suspected were intergrades (two referred to "*M. s. spixii* x *princeps*" and two referred to "*M. s. obscurus* x *princeps*"). Unfortunately, he did not cite specific specimens or explain why these specimens were classified as intergrades, and we could not evaluate their status.

In Bolivia, two clearly distinct species have been referred to *Micrurus spixii*. As we argue above, the differences between *M. s. obscurus* and *M. s. princeps* on the one hand and between *M. s. martiusi* and *M. s. spixii* on the other have been overstated or, at least, accorded too much significance. We therefore refer *Elaps princeps* Boulenger to the synonymy of *Micrurus obscurus* (Jan) **new combination** and *Micrurus spixii martiusi* Schmidt to the synonymy of *Micrurus spixii* Wagler. In Bolivia, these two species have been found in sympatry at Ri-

beralta, Beni department (compare NK 512 and UMMZ 63820). Two additional specimens, *M. spixii* from Tumi Chucua, Beni (USNM 280426) and *M. obscurus* from San Carlos, Pando (NK 259) are both from within 100 km of Riberalta. There is no apparent intergradation between these species in Bolivia where their ranges overlap.

The two species are easily separated on the basis of pattern. *Micrurus obscurus* differs from *M. spixii* in having a black interorbital band angled anteriorly where it crosses the eye and overlapping supralabial 3 and part of 4 (Fig. 8; see also Fig. 34 in Schmidt, 1953*b* and species accounts in Roze, 1996). The band is not present in *M. spixii*, and the anterior 1–5 supralabials have black posterior edges. The dorsal head scales in *M. spixii* are black with red or yellow margins and the parietals are nearly completely black. In *M. obscurus*, the snout scales are yellow with black margins and spots. In central Bolivia, the parietals of *M. obscurus* are immaculate or have black apices, whereas large black spots are present in the parietals of specimens from northern Bolivia and elsewhere in upper Amazonian South America. The first black ring on the body of *M. spixii* is an exterior ring and has a nearly vertical anterior margin, whereas the black ring is a middle ring and strongly projects anteriorly in *M. obscurus* [the first triad is occasionally complete in specimens from the Orinoco drainage of Colombia (Campbell and Lamar, 1989; Roze, 1996), however this condition has not been observed in Bolivia]. Finally, the mental and sometimes the flanking first or second infralabials are black and the posterior ventral surface of the head is immaculate in Bolivian *M. obscurus*. In the other subspecies, the pattern on the chin is quite different, with black blotches being most prominent on more posterior infralabials. Some specimens (e.g., AMNH 22277) of *M. spixii* also have a black mental. All but 2 (93%) of our sample of Bolivian *M. obscurus* have two-thirds of a triad on the tail, whereas most (57%) Bolivian *M. spixii* have one to one-and-a-third triad on the tail. Finally, some (1–7) exterior rings are incomplete and others are noticeably very short ventrally in Bolivian *M. obscurus*. Ventrally, the black rings are as long as or longer (e.g., USNM specimens) than they are dorsally and they are always complete on the body in *M. spixii*. As for other species of coralsnakes, rings in *M. spixii* may be incomplete (e.g., USNM 280426) when they traverse the vent.

Intraspecific concordance in several characters and sympatry between *M. spixii* and *M. obscurus* in Beni strongly indicates that these species do not interbreed. Contra Roze (1996), we do not believe that a case for intergradation has been made, and we have not observed any evidence of intergradation between these two well-differentiated and recognizable species.

Micrurus obscurus (as *M. spixii princeps*) has long been thought to be the largest coralsnake based upon measurements of CM 126. Griffin (1916) reported 1602 mm for this specimen and Schmidt (1953*b*) reported 1600 mm. These measurements are incorrect by more than 150 mm; this male specimen is 1413 mm (SVL 1345 mm, tail length 68 mm). A specimen of *Micrurus ancoralis* in the BMNH measured 1486 mm and may be the largest coralsnake (Roze, 1996).

Micrurus pyrrhocryptus (Cope)

(Fig. 10)

Elaps pyrrhocryptus Cope, 1862:347. HOLOTYPE (sex unknown) from “Vermejo River, Argentine Chaco” (=Río Bermejo, Chaco, Argentina, Scrocchi, 1990) (ANSP 5395). Peracca, 1895:19; Berg, 1898:29.



Fig. 10.—*Micrurus pyrrhocryptus* (UTA 51404) from Finca Dos Milanos, Chiquitos, Santa Cruz.

Elaps marcgravii (Wied-Neuwied): Boulenger, 1896:428; Peracca, 1897b:15.

Elaps Simonsii Boulenger, 1902a:338. HOLOTYPE female from "Cruz del Eje," Córdoba, Argentina (BMNH 1946.1.21.33).

Elaps frontalis (Duméril, Bibron, and Duméril): Lönnberg, 1902:461; Amaral, 1925:19; Bucher, 1980:158.

Micrurus pyrrhocryptus (Cope): Schmidt, 1936:199; Hoge and Lancini, 1960:12; Scrocchi, 1990:359; Cruz et al., 1992:104; Yanosky et al., 1993:163; Lavilla et al., 1995:126; Gonzales, 1998:49; Leynaud and Bucher, 1999:37; David and Ineich, 1999:152; Jorge da Silva and Sites, 1999:172.

Micrurus lemniscatus frontalis (Duméril, Bibron, and Duméril): Amaral 1944:92 (in part); Abalos and Nader, 1962:83; Abalos et al., 1964:267; Abalos and Mischis, 1975:74.

Micrurus frontalis pyrrhocryptus (Cope): Shreve, 1953:5; Barrio and Miranda, 1967:872; Roze, 1967:26; Roze, 1970:209; Hoge and Romano, 1973:125; Laurent and Teran, 1981:13; Roze, 1983:326; Golay, 1985:34; Campbell and Lamar, 1989:116; Golay et al., 1993:168.

Micrurus tricolor Hoge, 1956:67. HOLOTYPE male from "Garandazal" (=Carandazal according to Jorge da Silva and Sites, 1999), Mato Grosso do Sul (IB 16290). Strussman and Sazima, 1993:163; Jorge da Silva and Sites, 1999:176. [revised synonymy, see remarks]

Micrurus lemniscatus (Linnaeus): Abalos, 1961:70.

Micrurus fontalis (Duméril, Bibron, and Duméril): Fugler, 1986:57; Fugler and Cabot, 1995:60.

Micrurus frontalis tricolor (Hoge): Campbell and Lamar, 1989:116; Golay, 1993:168.

Micrurus pyrrhocryptus pyrrhocryptus (Cope): Roze, 1994:179; Roze, 1996:212.

Micrurus pyrrhocryptus tricolor (Hoge): Roze, 1994:179, 1996:212.

Diagnosis.—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal

scale usually divided; (6) first triad complete; (7) 5–12 red vertebrals separating first triad from parietals; (8) all dorsal head scales including parietals black, edged in white; (9) red rings with heavier black apices than white rings; (10) white rings longest dorsally, constricted or broken ventrally by black rings; (11) chin red with no to moderate black mottling and edging of scales; mental mostly or entirely red; (12) 6–14 triads on body, 1–1.67 on tail.

Description.—(Based on 9 females, 11 males, and 5 juveniles). *Micrurus pyrrhocryptus* is a large species; specimens in our sample were 264–1209 mm long (Jorge da Silva and Sites, 1999, report a maximum size of 1241 mm), the largest specimen being a male. The tails of females are 6.2–7.4% (6.7 ± 0.4 , 8) as long as their snout-vent lengths, and the tails of males are 5.9–8.1% (7.2 ± 0.9 , 10) as long as their snout-vent lengths. The head accounts for 1.5–2.4% (2.2 ± 0.3 , 22) of snout-vent length.

In our sample, all specimens had 2/2 postoculars and 1+1/1+1 temporals. One specimen had eight infralabials on one side only, whereas all others had 7/7 infralabials and supralabials. The prefrontals contact the supralabials in a single specimen (NK 882). Eye-nostril distance accounts for 18–37% (23 ± 5 , 15) of head length, and eye diameter accounts for 12–27% (16 ± 5 , 14) of head length. In this species, the supraocular is usually narrower than the frontal. However, the supraocular was 0.1 mm wider in one specimen (NK 2031). Variation in relative widths of these scales is considerable: the supraocular is 70–103% (84 ± 8 , 16) as wide as the frontal.

In three of our specimens (12%, 25), only the first three infralabials contact the first pair of chinshields on both sides; more often, the first four contact the first pair and only the fourth contacts the second pair. Four to six (5 ± 1 , 25) gulars and prementals separate the second pair of chinshields from the mentals. Females have 221–240 (229 ± 5 , 9) mentals and 20–26 (24 ± 2 , 8) subcaudals, whereas males have 220–246 (234 ± 8 , 12) mentals and 24–31 (28 ± 2 , 12) subcaudals. In three specimens (12%, 25) one to as many as nine subcaudals were entire.

The dorsal head and snout scales (internasals, prefrontals, frontal, parietals, oculars, nasals, rostral) are black with white bordering. Usually, the centers of these scales are immaculate, although white blotches may be present on some scales (e.g., AMNH 141357, white blotch on one prefrontal). The first three or four supralabials are mostly black with white margins. The temporals and last three supralabials range from being immaculate red (e.g., AMNH 141357) to having large black blotches (e.g., MCZ 20622). The infralabials, chinshields, and gulars are red and may be nearly immaculate (UTA 51404) or have diffuse to moderate (MCZ 20622) amounts of black blotching and edging of scales. The mental may also have some black pigment, but it is mostly red.

The black rings are longest ventrally where they project into the white rings, usually constricting them to one or two mentals. Except rarely (e.g., CM 2761; AMNH 141357), the white rings are complete; the black rings are always complete. Bolivian specimens have about the same number of body triads as conspecifics in Argentina and Paraguay (Jorge da Silva and Sites, 1999), however the distance to the first triad appears to be greater (Jorge da Silva and Sites, 1999, do not give a mean value for this meristic but provide a range of 5–7 vertebrals from the parietals to the first black ring). Two specimens (CBF 1203 with 12 and USNM 1186 with 14 body triads) had more than 11 body triads. In Bolivia, this species has 6–14 (8 ± 2 , 25) triads on the body and 1–1.67 (usually 1.33, 25)

triads on the tail. The first triad is separated from the parietals by 5–11.5 (8.5 ± 2.5 , 25) vertebrae.

The statement that “the middle black ring is at least twice (10–14 dorsal scales) the length of the external one (5–7 dorsal scales)” (Jorge da Silva and Sites, 1999, p. 174) does not apply to this species in Bolivia where relative lengths of the rings are highly variable. In one specimen (USNM 1186), the middle black rings (3 vertebrae long in the middle triad) were about the same size to slightly shorter than the external black rings (3.5 vertebrae long in the middle triad). The external rings were 2.5–5.5 dorsals long and 32–117% (62 ± 21 , 24) as long as the middle ring, which ranges from 3–11 vertebrae. Moreover, the red rings are never “almost the same length as the entire triads” (contra Jorge da Silva and Sites, 1999, p. 174). In three specimens (e.g., NK 524), the middle black rings and the red rings are about the same length. In the entire sample, red rings are 7.5–15.5 dorsals long, and the middle black rings are 22–107% (65 ± 21 , 24) as long as the red rings. The white rings are 1–3.5 vertebrae long and 36–105% (60 ± 21 , 24) as long as the external black rings.

Distribution.—Jorge da Silva and Sites (1999) discuss this species’ distribution outside of Bolivia. Within Bolivia, *Micrurus pyrrhocryptus* is restricted to the Gran Chaco, the band of high forest of the Tierras Bajas region, Chiquitanía, and the vicinity of Santa Cruz de la Sierra and Buena Vista (Fig. 11). In addition to our localities, Lönnberg (1902) examined specimens from “Tatarenda, Caiza, Bolivian Chaco” and Roze (1983) reported that the species occurs in lowlands near the type locality of *M. diana*.

BOLIVIA. CHUQUISACA. Luis Calvo: Pozo Camatindi (CBF 1203). **SANTA CRUZ.** Andrés Ibáñez: Santa Cruz de la Sierra (NK 511, 728, 882, 961, 1447). **Chiquitos:** NK 2035, UTA 51404 (Finca Dos Milanos). **Cordillera:** Aguaraigua (NK 1446), Camiri (USNM 118640), Izozog (NK 2025–26, NK 2031–32), 1 km N Gutiérrez (NK 543 (1 Km N of Gutiérrez)). **Ichilo:** Buena Vista (CM 2760, 2761, FMNH 16788, MCZ 20622). **Ñuño de Chávez:** Estancia San Miguelito (NK 1308). **Sara:** unknown (CM 2762). **Warnes:** Azusaquí (NK 125). **Unknown:** UMMZ 69553. **UNKNOWN:** NK 524, 654.

Remarks.—Although long considered to have its affinities with snakes of the *Micrurus frontalis* complex, the status of Hoge’s (1957) *Micrurus tricolor* has been the subject of debate. It has been considered a separate species (Strussman and Sazima, 1993; Jorge da Silva and Sites, 1999), a synonym of *M. pyrrhocryptus* (Hoge and Lancini, 1960; Scrocchi, 1990), or a subspecies of either *M. frontalis* (Roze, 1983; Golay, 1985; Campbell and Lamar, 1989) or *M. pyrrhocryptus* (Roze, 1994; 1996).

Jorge da Silva and Sites (1999) provide a thoughtful review of the *Micrurus frontalis* complex. Refreshingly, their analysis is based on carefully defined methodological procedures and clear statements as to their concept of species. The number of specimens examined by the authors and their lab assistants is impressive. Most of the specimens examined in their study (many in Brazilian museums) were not included in this study; however we did examine the same specimens in the Museo “Noel Kempff Mercado,” the Fundación Miguel Lillo, and several museums in the United States.

In most instances, we agree with the findings of Jorge da Silva and Sites (1999); however, they are incorrect regarding the distinctiveness of *Micrurus tricolor*. Jorge da Silva and Sites (1999) took issue with the opinions of some revisors, stating, “the biggest problem in accepting Scrocchi’s (1990) and Roze’s (1994, 1996) taxonomic arrangement is that *M. tricolor* is not an isolated population in Mato Grosso do Sul, but it extends into Bolivia where it is sympatric with *M. pyrrhocryptus* and possibly *M. diana*.” This statement is based on a single Bo-

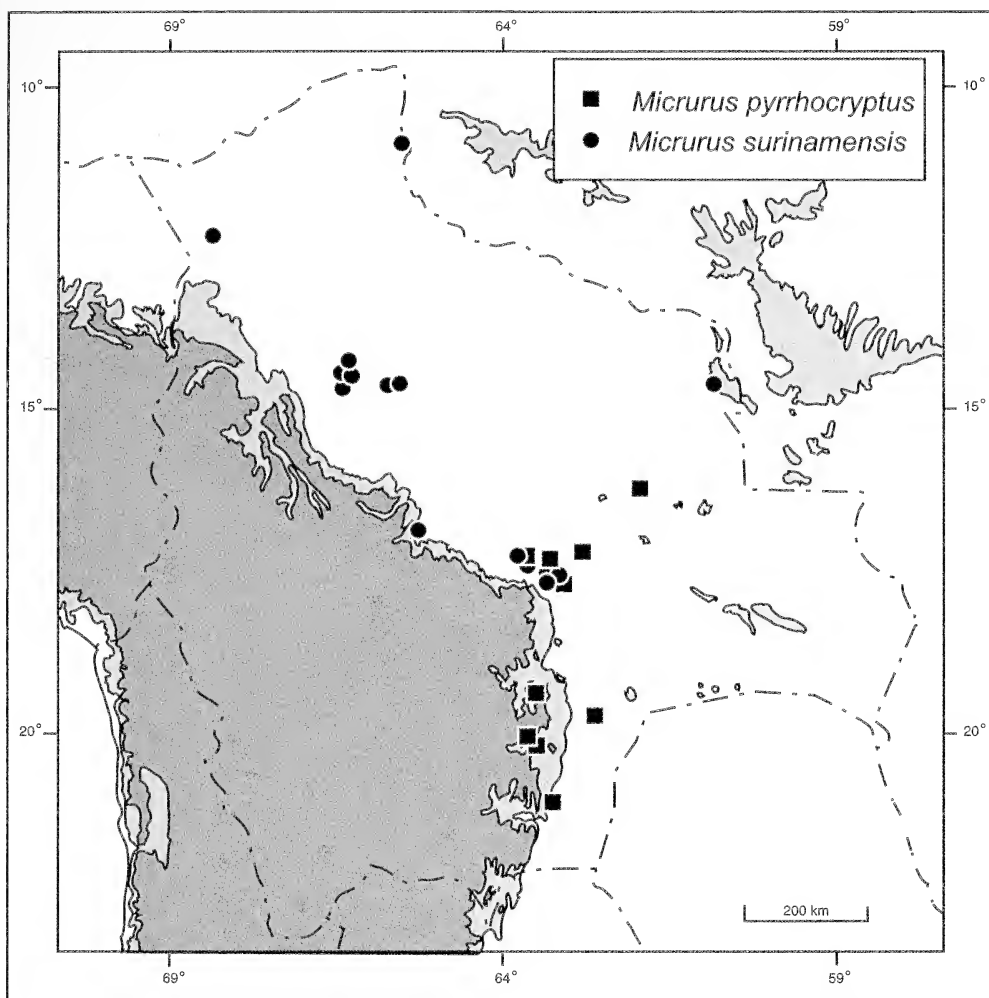


Fig. 11.—Distribution of *Micrurus pyrrhocryptus* and *M. surinamensis* in Bolivia.

livian specimen that these authors referred to *M. tricolor*: NK 543 (Fig. 12) from 1 km N. of Gutiérrez, Santa Cruz, Bolivia.

This specimen (NK 543) does not have diagnostic features of *Micrurus tricolor* (characters from Jorge da Silva and Sites, 1999, of *M. tricolor* in parentheses) that might be used to distinguish this species from *M. pyrrhocryptus*. All of the black snout scales have prominent white margins (“black snout covering all scales with very little white bordering, which when present is mostly restricted to the supralabials” and “frontal, supraoculars, and parietals are completely black”). Nearly all white scales in the triads have black tips (white scales in triads “immaculate”). In NK 543, the first triad is separated from the parietals by 8 dorsals, and this value is one scale higher than the narrow range of 5–7 dorsals Jorge da Silva and Sites (1999) report for *M. pyrrhocryptus*. However, variation in this character is much greater than the data of Jorge da Silva and Sites (1999) indicate.

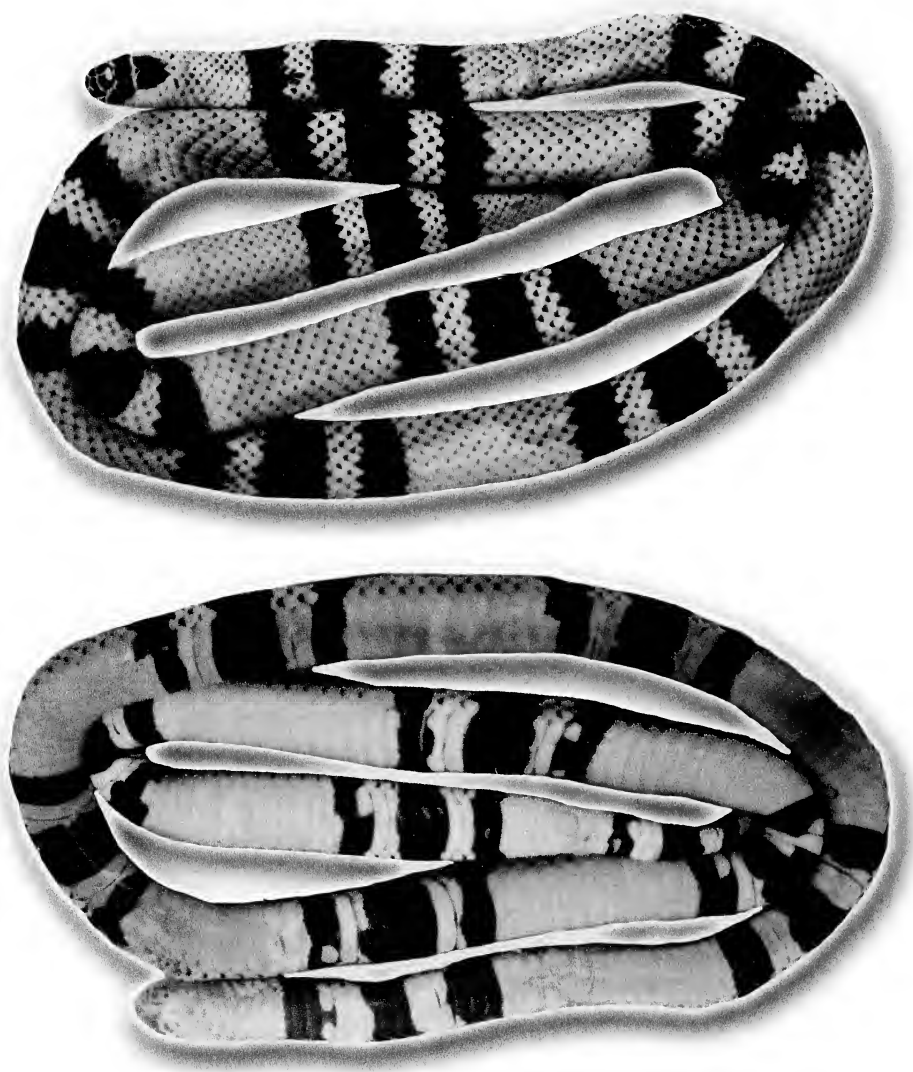


Fig. 12.—Specimen of *Micrurus pyrrhocryptus* (NK 543 M) misidentified as *M. tricolor* by Jorge da Silva and Sites (1999).

Among our sample, the parietals are separated from the first triad by 4–16 dorsals (8 or more dorsals in 59% of the specimens).

If sympatry of the two species is the real “problem” with synonymization, we wonder why no Bolivian *Micrurus pyrrhocryptus* were examined by Jorge da Silva and Sites (1999, see their appendix) when the same authors visited museums (e.g., Museo Noel Kempff) or at least borrowed specimens from museums (MCZ, FML) containing specimens of Bolivian *M. pyrrhocryptus*.

We have established that these two taxa are not sympatric and that *Micrurus tricolor* is not known from Bolivia. The remaining question is whether characteristics of the isolated Mato Grosso population are distinctive enough to warrant its recognition as a full species. Our concept of species is equivalent to that voiced by Jorge da Silva and Sites (1999; see also Frost and Hillis, 1990), and we have few complaints about their use of concordance (Avise and Ball, 1990) as a criterion for recognizing species. From Jorge da Silva and Sites' monograph, readers will conclude that *M. tricolor* could be recognized as distinct from *M. pyrrhocryptus* due to concordance of two characters: black snout scales with very little white bordering (vs. prominent white bordering in *pyrrhocryptus*) and white rings "immaculate" (vs. white rings "always black tipped"). Characterizations of the amount of black pigmentation in the rings are somewhat exaggerated. Frequently in *M. pyrrhocryptus* (e.g. NK 2031–32; UTA 51404), the first white ring is nearly immaculate, the second ring has a few short black apices, and more posterior white rings have increasing amounts of black. Only on the posterior one-third of the body and on the tail does every white scale possess a black apex (see also, Fig. 27b and c of Sites and Jorge da Silva, 1999). Similarly, some white scales have black apices increasingly on the posterior portion of the body of *M. tricolor*. Scales with black apices are clearly visible in all but the first two triads of the holotype (figure 1 on p. 71 of Hoge, 1957, and figure 31 of Jorge da Silva and Sites, 1999). The amount of black apices present in white rings is notoriously variable within many species of coralsnakes: *M. frontalis* (Jorge da Silva and Sites, 1999), *M. lemniscatus* and *M. serranus* (this study), to name a few. Extent of white bordering of dorsal head scales is quite variable in several species of the *M. frontalis* complex. Regional variation in these traits should be expected.

Jorge da Silva and Sites (1999) use multivariate analyses to support their taxonomic conclusions, and the results of these analyses are illustrated in their figure 2. In this figure, the error bars for females of *Micrurus pyrrhocryptus* and *M. tricolor* overlap substantially along both canonical variables. Males are partially separated along canonical variable 1 only. Inspection of the eigenvalues in table 3 of Jorge da Silva and Site's study shows that this variable is most influenced by middle black ring length and total number of triads. Jorge da Silva and Sites report that these same two variables were negatively correlated in a univariate analysis, and this fact explains the opposite signs of the corresponding eigenvalues. Essentially, the two variables seem to be a redundant expression of the same phenotypic trait: increase in number of triads requires that the middle black rings be shorter. The multivariate techniques do not uncover differences in these putative species. Above, we call attention to overlap in the error bars of females. We also point out that number of triads (and, therefore, length of the middle black ring) is much more variable in *M. pyrrhocryptus* than Jorge da Silva and Sites' data indicate, so that the apparent separation of males for canonical variable 1 would likely break down with the inclusion of more data.

Between *Micrurus pyrrhocryptus* and *M. tricolor*, only minor differences in coloration remain as potentially diagnostic characters: the amount of white bordering of the head scales and the amount of black pigment in the rings differ in degree only. Contrary to the claims of Jorge da Silva and Sites (1999), these taxa do not occur in sympatry, and we see no compelling evidence for recognition of them as distinct species. We follow Roze (1983, 1994, 1996), Golay (1985), and Campbell and Lamar (1989) in recognizing the Mato Grosso population as a subspecies: *Micrurus pyrrhocryptus tricolor* (Hoge).

As pointed out in the description, several meristics of the Bolivian specimens are at odds with Jorge da Silva and Sites' (1999) characterization of *Micrurus pyrrhocryptus*. The most atypical specimen in our sample (USNM 118640) was collected by Raymond M. Gilmore from "Camiri, 5 km S of Chorati, 800 m" (=Choreti) in the Gran Chaco of southern Santa Cruz. This specimen is unusual in having 14 body triads and the external black rings being the same size or slightly longer than the middle black ring.

We assign the specimen to *Micrurus pyrrhocryptus*, because its dorsal head and snout scales are black edged in white, seven vertebrae separate the first triad from the parietals, and the red and white rings have prominent black apices. In their diagnosis, Jorge da Silva and Sites (1999) state that *M. pyrrhocryptus* has 6–11 body triads, however in their remarks they say "the sample of *M. pyrrhocryptus* included in this study shows only three specimens with 12, 13, and 14 body triads respectively, and the majority of specimens have between 6 and 11 triads." Therefore, the diagnosis is misleading and should have included the known range of body triads with a qualifying statement that the species usually has 6–11 triads. We doubt that the USNM specimen is either *M. frontalis* or *M. baliocoryphus*, because the known distributions of both species are very distant from Camiri. These species reportedly differ from *M. pyrrhocryptus* in having white chins, however the USNM specimen is in poor condition, and we cannot determine the original color of its chin. Jorge da Silva and Sites (1999) fail to provide information on two potentially diagnostic features of *M. baliocoryphus*: number of vertebrae to the first triad and presence or absence of black pigment in the white rings. They state that in *M. baliocoryphus* the middle black ring is "at least twice as long" as the external black rings, however this statement is almost certainly an exaggeration as seems to be the case for a similar claim regarding *M. pyrrhocryptus*. The statement is not consistent with specimens Jorge da Silva and Sites examined. In FML 1986 (formerly CHINM 2870. The Colección Herpetologica del Instituto Nacional de Microbiología Carlos G. Malbrán gave this specimen to the Fundación Miguel Lillo, and the two tag numbers do not apply to separate individuals as Jorge da Silva and Sites thought, p. 164), the middle black ring is only slightly longer (2.5 vertebrae) than the external rings (2 vertebrae). Regarding this specimen, Jorge da Silva and Sites (1999, p. 164) write "The specimens (CHINM 2870 M and CHINM 2871 M) mentioned by Scrocchi (1990) as intermediary forms are in fact *M. baliocoryphus*, and this has been corroborated by an additional specimen (FML 1986 M)." Like *M. altirostris*, the external and middle black rings are about the same size, and, on the basis of this character, Scrocchi's (1990) opinion is understandable. In the FML specimen, the white rings of the first two triads are nearly immaculate, but in the remaining triads about one-half to two-thirds of the white scales have prominent black apices (i.e., some white rings are as heavily pigmented as the red rings). Except for relative widths of the rings, the specimen has the characteristics of *M. baliocoryphus*: 3.5 vertebrae separate the parietals from the first triad (vs. 1–2 in *M. altirostris*), the chin has only moderate amounts of black pigment (heavy in *M. altirostris*), and there are 11 (vs. 13–18 in *M. altirostris*) body triads.

Micrurus serranus, **new species**
(Fig. 6 A, 6C, 13)

Micrurus frontifasciatus (Werner): Campbell and Lamar, 1989: 116 (in part), figure 55; Fugler and Cabot, 1995: 60; Roze, 1996: 175 (in part), color plate 28. [new synonymy]



Fig. 13.—*Micrurus serranus* new species (Holotype, UTA 34561 M) from 3 km N of Samaipata, Florida, Santa Cruz.

Holotype.—A male specimen, UTA 34561 (collector's tag M. B. Harvey 1960) found by Michael B. Harvey, 3 km N of Samaipata on the road to Mairana, Florida Province, Santa Cruz, Bolivia, 14 Feb. 1992.

Paratypes (39).—Museum numbers are followed by the specimen's sex, its collector, date collected, and locality. The canton within Florida province follows the specific locality when that locality could not be located in the *Atlas Estadístico de Municipios* (Fig. 5). **BOLIVIA. SANTA CRUZ. Caballero:** NK 1565 (M, A. Medellín, 4 Feb. 1998, San Juan del Potrero), NK 2020 (F, S. Medellín, 26 Nov. 1999, San Juan del Potrero). **Florida:** UTA 34562 (F, M. Harvey, 13 Feb. 1992, Yungas near Mairana, 18.09°, 63.91°W) NK 636 (F, W. Romero, 24 Oct. 94, Pampa Grande), 981 (F, S. Zambrana, 5 Dec. 1996, Algodonal), 1317 (F, N. Ferrufino, 22 Mar. 1997, Mairana), 1442 (F, G. Cardoso, 27 Aug. 1997, Agua Clara, Mataral), 1472 (F, M. Mendoza, 8 Nov. 1997, Algodonal), 1508 (M, I. Diaz, 22 Oct. 1997, Mataral), 1510 (M, M. Cuéllar, 13 Mar. 1998, Mairana), 1517 (M, D. Guzmán, 18 Jan. 1998, Zanjón, Mataral), 1551 (F, A. Langer, 26 Dec. 1997, Mairana), 1552 (M, Z. Rodriguez, 28 Feb. 1998, Becerro), 1555 (M, F. Morón, 6 Dec. 1997, "Villa Merced" = Villa Mercedes, Mataral), 1556 (M, F. Langer, 6 Dec. 1997, Pampa Grande), 1557 (M, A. Rodriguez, 25 Dec. 1997, Becerro), 1558 (F, T. Sejas, 13 Feb. 1998, Zanjón, Mataral), 1561 (F, A. Gutiérrez, 22 Nov. 1997, Pampa Grande), 1564 (M, J. Chilo, 23 Dec. 1997, Palmasola), 1581 (M, I. Zambrana, 29 Nov. 1997, Algodonal), 1584 (F, T. Sejas, 8 Nov. 1997, Zanjón, Mataral), 1587 (F, M. Olmos, 31 Oct. 1997, "Villa Merced" = Villa Mercedes, Mataral), 1589 (F, A. Alaudio, 28 Mar. 1998, Algodonal), 1605 (M, S. Rojas, 6 Jan. 1998, El Millo), 1617 (M, O. Calla, 12 Mar. 1994, Pampa Grande), 1706 (F, A. Langer, 9 Mar. 1997 "entre Mairana y Samaipata"), 1721 (M, A. Ayala, 7 May 1998, Mataral), 1723 (M, N. Terrazas, 8 Apr. 1998, "Villa Merced" = Villa Mercedes, Mataral), 1746 (F, I. Zambrana, 5 Apr. 1998, Algodonal), 1752 (M, W. Peña, 11 May 1998, Zanjón, Mataral), 1865 (M, F. Sejas, 10 Jan. 1999, Palmasola), 1866 (M, F. Olmos, 23 Mar. 1998, Pampa Grande), 1867 (M, Z. Rodriguez, 20 Jan. 1999, Becerro), 1868 (M, M. Rojas, 17 Feb. 1998, Pampa Grande), 1869 (M, D. Ayala, 5 Jun. 1999, Santa Rosa de Lima, Palos Blancos), 1944 (F, G. Lazarte, 28 Oct. 1999, Algodonal), 1945 (F, V. Arroyo, 5 Oct. 1999, Pampa Grande), 2009 (F, A. Rojas, 3 Mar. 1998, El Millo, Pampa Grande), 2030 (F, A. Langer, 29 Nov. 1997, Pampa Grande).

Referred Specimens (67).—CBF 1743, NK 447, NK 481, NK 494, NK 590, NK 678, NK 694, NK 754, NK 855, NK 868, NK 883, NK 897–98, NK 916, NK 945, NK 982, NK 989, NK 1065, NK 1249–50, NK 1260–61, NK 1318–1323, NK 1424, NK 1441, NK 1471, NK 1502–03, NK 1545–47, NK 1550, NK 1553–54, NK 1559–60, NK 1563, NK 1568, NK 1580, NK 1583, NK 1590, NK 1603, NK 1613, NK 1639–40, NK 1643, NK 1722, NK 1724, NK 1753, NK 1779, NK 1852–53, NK 1893, NK 1949, NK 1963, NK 1979, NK 1988, NK 2000, NK 2007–08, NK 2013, NK 2016.

Diagnosis.—*Micrurus serranus* is a small (maximum size to 822 mm total length) coralsnake with the following characteristics: (1) Dorsal pattern of white, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually (95%) separated from chinshields by medial contact of first pair of infralabials; (5) anal scale usually (90%) divided; (6) first triad complete; (7) 1–6 red vertebrals separating first triad from parietals; (8) dorsal surface of head black with white (pale yellow in life) band crossing snout; margins of scales within white ring edged in black; parietals partly red; (9) extent of black pigment in red and white rings variable, but white rings with more black pigment than red rings; (10) white rings longest dorsally, constricted or broken ventrally by black rings; (11) parietals red with black pigment concentrated anteriorly; (12) 10–14 triads on the body, 0.67–1.67 on the tail; (13) black rings almost always longer than white rings; (14) black pigment present on mental, anterior infralabials, and chinshields; white or pale yellow pigment may also be present in the same region.

Comparisons.—In that all three species have white bands across their snouts, the new species may be confused with *Micrurus lemniscatus* and *M. filiformis* (characteristics in parentheses). Unlike these Amazonian species, the white rings of *M. serranus* are longest dorsally and invaded or interrupted by the black rings midventrally (white rings longest ventrally, not invaded by black rings). Also,

scales in the white band across the snout are edged in black (white band across snout immaculate). In addition, the snout of *M. serranus* is noticeably more acuminate than the rounded snouts of *M. filiformis* and *M. lemniscatus* (Fig. 6).

Four species in the *Micrurus frontalis* complex have black and white snouts and, though rarely the case, occasional specimens in the *M. frontalis* complex may appear to have a white band across the snout. Unlike the new species, the parietals are black in *M. baliocoryphus*, *M. diana*, *M. frontalis*, and *M. pyrrhocyptus*. *Micrurus serranus* usually does not show a tendency toward melanism and has fewer triads (10–14 vs. 13–18) than the distantly allopatric species *M. altirostris*. Black pigment is concentrated anteriorly on the parietals of the new species, whereas it is concentrated posteriorly on the parietals of *M. altirostris*. Although *M. brasiliensis* has black pigment concentrated anteriorly in its parietals and has about the same number of triads as the new species, the white rings of *M. brasiliensis* are as long or longer than the black rings and scales within the white rings are edged weakly in black. In the new species, dorsals in the white rings bear heavy black margins and the white rings are usually shorter than the black rings.

Other cis-Andean triadal coral snakes are either distantly allopatric or morphologically distinct from *Micrurus serranus* (characters in parentheses). *Micrurus decoratus* from the Atlantic coast of Brazil usually has a higher number of body triads (12–19 vs. 10–14) and reduced black pigmentation in the yellow rings (white to pale-yellow rings with heavy black edging of dorsals). *Micrurus hemprichii* has an entire anal plate (divided), black dorsal head scales including the parietals (white band across snout and red and black parietals), and few body triads consisting of long black rings separated by short orange rings (5–10 vs. 10–14 triads with black rings usually slightly longer than white or pale yellow rings). *Micrurus ibiboboca* usually has fewer body triads (7–10 vs. 10–14), and the ventral surface of its head is red except for occasional specimens with black pigment restricted to the mental (chin always with some black pigment on the mental, anterior infralabials, and chinshields). In *M. isozonus*, the snout is black and usually lacks a white band (white band always present), the parietals are red-orange with black apices (red and black with black pigment concentrated anteriorly), the ventral surface of the head is mostly red and white with very reduced black pigment (heavy black pigment), and the triads are separated by red-orange rings (red) and the light colored rings of the triads are yellow (white to pale yellow). *Micrurus obscurus* and *M. spixii* both have fewer body triads (4–10 vs. 10–14) and the first triad is incomplete. *Micrurus surinamensis* has a red head with black-edged scales (black cap with white ring), and fewer body triads (5–8.67 vs. 10–14). In *M. surinamensis*, only one supralabial (two) enters the orbit.

Description of Holotype.—The holotype appears to be an adult based on its size relative to other specimens in the type series and because its hemipenes are well developed. The head is round in lateral profile and subacuminate in dorsal aspect. Its length accounts for 2.3% of snout-vent length. The eye is relatively small; its diameter is 13% of head length and its distance to the nostril is 24% of head length. The rostral is about as wide as the mental and 71% as high as wide. It is followed by pentagonal internasals and prefrontals. The internasals contact the postnasal and are 78% as long as wide. The prefrontals are only slightly wider than long and are separated from the supralabials by broad contact between the postnasal and the single, high preocular. The prenasal is twice as large as the postnasal. The frontal is pentagonal and one-half again as long as

wide. It is flanked by subrectangular supraoculars, each 1.6 times as long as wide. The parietals are 64% as wide as long and broadly contact the uppermost and largest of two postoculars. They are separated from the supralabials by 1+1 temporals. A single large vertebral fills the space between the parietal tips. The specimen has 7/7 supralabials; supralabial three barely contacts the postnasal, three and four enter the orbit, and six is separated from the lower postocular by broad contact between the postocular and supralabial five.

The mental is 73% as long as wide and separated from the first pair of chinshields by broad contact between the first pair of infralabials. A weak mental groove, three times as long as the mental, separates the chinshields. The first pair of chinshields is rectangular and relatively short, being 71% as wide as long; the second pair has rounded posterior margins and is 53% as wide as long. There are 7/7 infralabials, the first four contacting the first pair of chinshields and the fourth contacting the second pair. Two gulars and two preventrals separate the chinshields from 218 ventrals and 23 subcaudals. Subcaudals 2-3 and 8 are entire; the anal scale and remaining subcaudals are divided.

In preservative (70% ethanol after buffered 10% formalin), the dorsal pattern consists of white (pale yellow, in life), red, and black rings. The rostral, prenasal, and supralabial 1 are entirely black. A white blotch is present at the anterior juncture of the internasals, and the remainder of these scales is also uniformly black. The first white band on the head is angled antero-ventrally and overlaps the prefrontals, the anterior edge of the frontal, the anterior edge of the supraoculars, the postnasals, and the anterior halves of the preoculars. On one side, the white pigment extends onto the dorsal edge of supralabial two and anterior corner of supralabial 3, whereas on the other side supralabials 1-5 are entirely black. Scales within the white prefrontal band have prominent black edges. A black band follows the white prefrontal band to cross the eye and overlap most of the frontal, the anterior halves of the parietals, most of the supraoculars, one-half of each preocular, the postoculars, the anterior halves of the first temporals, and supralabials 3-5. This band does not extend onto the lower jaw. The remainder of the dorsal surface of the head (i.e., the posterior halves of the parietals, the posterior halves of the first temporals, the second temporals, and supralabials 6-7) is red. Except for the sixth supralabials, the dorsal head scales in the red band have black apices.

Ventrally, the mental and most of the first infralabials and first chinshields are black. A small black blotch is present on each of the second infralabials near the mental groove. Nonmelanic portions of infralabials 1-2 and the first pair of chinshields are white. The remaining scales on the ventral surface of the head are immaculate red.

The first triad is complete and is separated from the parietals by a single red vertebral. Rings in the first triad are symmetrical in size: the exterior rings are three vertebrae long, the white rings two vertebrae long, and the middle black ring five vertebrae long. Ventrally, the first black ring overlaps most of the first preventral and all of the first and second ventrals. There are fourteen triads on the body and one complete triad on the tail. A red ring overlaps the anal plate, and the tip of the tail is also red. Throughout the body and tail, the anterior edge of each black ring is straight, i.e., posterior portions of some white or red scales are overlapped by black rings. However, the posterior edge of black rings appears jagged; black scales are entirely black, and the jagged appearance is due to the staggered arrangement of dorsals. In the white rings most scales bear heavy black

apices and edging, whereas only a few scales in each of the red rings bear much weaker black apices and these scales tend to be concentrated vertebally and in the middle of the red rings. Ventrally, red rings are immaculate. Ventrals and paraventrals of the white rings have black edges. In most triads, a single round white spot is positioned laterally in the last ventral of exterior black rings. The black rings invade the white rings and completely interrupt them in the fifth and sixth triad.

In the middle triad, the red ring is 2.5, the exterior black rings two, the white rings two, and the middle black ring three vertebrae long. The caudal triad is relatively longer than those on the body due to an increased length of the middle ring: whereas, the white and exterior black rings are both three vertebrae long, the middle ring is six vertebrae long.

Measurements (in mm) of holotype: snout-vent length 480, tail length 34, head length 10.90, eye-nostril distance 2.58, eye diameter 1.42, length of red ring in middle triad 5.78, length of exterior black ring in middle triad 5.72, length of white ring in middle triad 4.05, length of middle black ring in middle triad 7.77, rostral width 2.8, rostral height 2.0, internasal width 1.89, internasal height 1.47, prefrontal width 2.24, prefrontal height 2.18, frontal width 2.42, frontal length 3.69, supraocular width 1.9, supraocular length 3.1, preocular height 3.12, preocular length 4.84, mental width 2.19, mental length 1.54, first chinshield width 1.5, first chinshield length 2.12, second chinshield length 2.84, length of mental groove 4.66.

Variation.—Except where noted, this section is based on the type series and does not include data from referred material. *Micrurus serranus* usually possesses the cephalic squamation pattern typical of most congeners. Among the type series, 1+1 temporals were usually (94%, 40) present, although three specimens had 1+2 temporals on one side only, and one specimen had 2+2 temporals on one side. One preocular and two postoculars were almost invariably present (NK 1558 had one postocular on one side only), and the supralabials and prefrontal were always separated by contact between the preocular and postnasal. Supralabials and infralabials numbered seven, except in NK 1867 which had six supralabials on one side. Supralabials three and four invariably enter the orbit. In two specimens, the mental contacts the anterior pair of chinshields, but these scales are otherwise separated by medial contact between the first pair of infralabials. Five percent of the time, only the first three infralabials contact the first chinshield; usually, infralabials 1–4 contact the first and infralabial 4 contacts the last chinshield. Four paratypes (10%, 40) had entire anal plates.

Sexual dimorphism could not be demonstrated statistically for relative body and tail lengths, number of ventrals, or number of subcaudals. The largest specimen was a male (NK 982, referred specimen) and had a snout-vent length of 763 mm and tail length of 59 mm; the largest female (NK 636) had a snout-vent length of 618 mm and tail length of 36 mm. The tail is 6.8–8.5% (7.5 ± 0.5 , 21) as long as the body in males and 5.8–8.2% (7.3 ± 0.6 , 19) as long in females. The head accounts for 2.0–2.5% of snout-vent length in both males (2.2 ± 0.1 , 21) and females (2.1 ± 0.7 , 17). Ventrals are separated from the second pair of chinshields by 3–5 (4 ± 1 , 40) gulars and preentrals and range from 209–220 (215 ± 3 , 21) in males and from 208–221 (216 ± 3 , 19) in females. Nearly half of all specimens (45%, 40) had 1–20 (2 ± 4) entire subcaudals; subcaudals ranged from 22–26 (24 ± 1 , 40) in males and 18–27 (23 ± 2 , 40) in females.

Micrurus serranus has 10–14 (11.8 ± 1.1 , 40) complete triads on the body.

Usually (63%, 40), one and one-third triad is present on the tail and the tip of the tail is black. Less commonly, one (18%, 40), one and two-thirds (16%, 40), or two-thirds (one specimen, 2.5%, 40) triad is present on the tail. The first triad is always complete and is separated from the parietals by 1–5.5 (3.1 ± 1.0 , 40) dorsals. In the midbody triad, the red ring extends for 2.5–10.5 (5.5 ± 1.6 , 40) dorsals, the first black ring extends for 2–5 (2.9 ± 0.5 , 40) dorsals, the first white ring extends for 1.5–3.5 (2.3 ± 0.4 , 40) dorsals, and the middle black ring extends for 2–4.5 (3.4 ± 0.7 , 40) dorsals. Usually, the red ring is as long as or longer than the middle black ring (number of dorsals in red ring/dorsals in middle black ring = $0.83\text{--}5.25$, 1.70 ± 0.81 , 40). A single specimen (UTA 34561) had the red ring slightly shorter (2.5 dorsals) than the middle black ring (3 dorsals). The first and last black rings of the triads are usually (87.5%, 40) the same size as or shorter than the middle ring (number of dorsals in first black ring/dorsals in middle black ring = $0.5\text{--}1.7$, 0.87 ± 0.23 , 40) and usually (except in UTA 34562) longer than the white rings. Similarly, the white rings are almost always (NK 1472 being the only exception) shorter than the middle black ring (number of dorsals in first white ring/dorsals in middle black ring = $0.4\text{--}1.2$, 0.68 ± 0.19 , 40).

All specimens have the distinctive pale-yellow (white in preservative) band with black-edged scales across the prefrontals. The parietals may be from one-fourth to nearly completely black. The anterior portion of each parietal is always black; generally the apices are black, but they may be immaculate or the red portions of the parietals may have irregular black blotches in them. The anterior chin (mental, anterior infralabials, chinshields) always bears some pigment (minimally the mental and anteriormost infralabials have black blotches or are entirely black), and most specimens were classified as having moderate (65%, 40) to heavy (25%, 40) pigmentation on the anterior chin. Frequently, the pale yellow band on the snout extends across the infralabials and chinshields (i.e., the chin may be black and red or have some pale yellow pigment). The posterior infralabials, posterior chinshields, gulars, and preventrals are usually red. Ventrally, the white rings are shortest and the black rings frequently interrupt the white ring. Red rings are almost always immaculate ventrally. Dorsally, the amount of black in the red rings appears to vary continuously with some specimens (e.g., NK 1722) having nearly immaculate red rings and others (e.g., NK 1323) having nearly every red scale in the rings with a black apex. The amount of black in the white rings is always noticeably greater than in the red rings, and the scales of the white rings always have black apices.

Etymology.—The specific epithet *serranus* is an adjective derived from the Spanish adjective *serrano*, meaning highland and refers to the species' restricted range at high elevations in intermontane valleys of Santa Cruz and Cochabamba, Bolivia.

Natural History.—Perhaps the most notable characteristic of *Micrurus serranus* is the apparently high proportion of males in the sample: they were ten times more common than females (all adult females were included in the type series). Parker and Plummer (1987) recently reviewed sex ratios in snakes and found that male-biased sex ratios at birth are rare and are documented in only four species. However, male snakes often predominate in samples during periods of high sexual activity. Few specimens in the type series or referred material were collected by us, and more research is required to identify the cause of this skewed sex ratio.

Most specimens of *Micrurus serranus* were heavily infested with mites. NK 1546 was heavily damaged when collected, and we note the presence of the tail

of an unidentified *Leptotyphlops* protruding from its belly. NK 1510 was found eating a specimen of *Amphisbaena cegei*. Specimens were encountered throughout the year, although most specimens were collected in December, January, and March, near the beginning and end of the rainy season. In 1991, Harvey found two specimens (UTA 34561–62) on the road after a heavy rain.

Red, black and white banding on the head and neck of the sympatric elapomorphine *Apostolepis multicincta* resembles the pattern on the head of *Micrurus serranus*, and these two venomous species may be part of a Müllerian mimicry system (Harvey, 1999).

Distribution.—*Micrurus serranus* appears to be endemic to the intermontane valleys of Santa Cruz and Cochabamba where it occurs at elevations between 1200 and 2150 m. The vast majority of specimens have been collected from the cantons of Mataral and Pampagrande in Florida province, Santa Cruz. The species' existence in Cochabamba is documented by a photograph in Campbell and Lamar (1989) of a specimen from "Aguiles" (= Aiquile, canton Aiquile, Campero province), 2150 m.

The vegetation of the intermontane valleys of Santa Cruz bears a strong resemblance to that of the Gran Chaco (Navarro, 1994). The type locality is characterized by sandy soils with scattered rock outcrops. At a meteorological station in Mairana (1350 m), average annual temperature is 20.9°C and average annual precipitation 575.4 mm. Much of the native vegetation at collecting sites has been altered by agricultural practices.

Remarks.—Harvey (1999) discussed the endemic herpetofauna of intermontane valleys of central Bolivia and noted the existence of apparent pairs of sister species with one species occurring in the Andean valleys and another in the Gran Chaco. If the pattern holds for the new species, we predict that its evolutionary affinities lie with the *Micrurus frontalis* complex. However, the new species appears to be more similar to distantly allopatric species such as *M. brasiliensis*, *M. diana*, and *M. frontalis* than to the Chacoan species *M. pyrrhocryptus*.

Micrurus spixii Wagler
(Fig. 8B, 8D)

Micrurus Spixii Wagler, 1824:48. HOLOTYPE male, Rio Solimões, Amazonas, Brazil (ZSMH 209/0).

Elaps Spixii (Wagler): Kaup, 1825:593.

Coluber Marcgravii (Wied-Neuwied): Fitzinger, 1826:901.

Elaps Marcgravii (Wied-Neuwied): Fitzinger, 1826:901; Wagler, 1830:193.

Elaps corallinus (Merrem): Schlegel, 1837 (in part); Jan, 1859:275; Jan, 1863a:112.

Elaps spixii (Wagler): Boulenger, 1896:427 (in part).

Elaps ehrhardti Müller, 1926:198. HOLOTYPE female, "Manacapurú am Solimões, Brasilien" (=Manacapurú, Rio Solimões, Brazil; ZSM 140/1925) [Amaral (1930a:53) mistakenly thought this name was synonymous with *Micrurus lemniscatus*].

Micrurus spixii (Wagler): Amaral, 1930b:112; Amaral, 1930c:232; Schmidt, 1936:198 (in part); Amaral, 1948b:159; Hoogmoed, 1979:277; Vanzolini, 1986:24; Fugler, 1986:58 (in part); Fugler and Cabot, 1995:60 (in part).

Micrurus spixi spixi (Wagler): Schmidt, 1953b:175; Golay et al., 1993:181.

Micrurus spixi martiusi Schmidt, 1953b:175. HOLOTYPE male, "Santarem, Pará, Brazil" (MCZ 2612). Golay et al., 1993:181 [new synonymy, see remarks under *Micrurus obscurus*].

Micrurus spixii martiusi (Schmidt): Roze, 1967:42; Roze, 1970:218; Hoge and Romano, 1973:129; Cunha and Nascimento, 1982:21; Roux-Esteve, 1983:89; Roze, 1983:335; Cunha et al., 1985:71; Campbell and Lamar, 1989:146; Roze, 1996:216.

Micrurus spixii spixii (Wagler): Roze, 1967:42; Roze, 1970:217; Hoge and Romano, 1973:129; Hoogmoed and Gruber, 1983:334; Roze, 1983:334. Nascimento et al., 1988:56; Campbell and Lamar, 1989:146; Roze and Jorge da Silva, 1990:174; Jorge da Silva, 1993:73; Roze, 1996:215.

Diagnosis.—(1) Dorsal pattern of yellow, red, and black triads; (2) hemipenis and tail relatively short; (3) two supralabials entering orbit; (4) mental usually separated from chinshields by medial contact of first pair of infralabials; (5) anal

scale usually divided; (6) first triad incomplete: one black ring on neck, its anterior margin nearly vertical; (7) dorsal scales of head (including parietals) black with light edges; (8) scales in yellow rings with heavier black apices than scales in red rings; (9) black rings about as long dorsally as ventrally, complete except for black ring straddling the vent; (10) mental usually immaculate, some black edging of more posterior scales on underside of head; (11) 5.33–7.67 (4–9 in specimens from outside Bolivia, Roze, 1996) triads on body and 0.67–1.33 triad on tail.

Description.—(Based on 4 males and 3 females). *Micrurus spixii* is a large species, three of our seven specimens exceed one meter, NK 60 being the largest at 1233 mm. The tail is 5.8–7.2% (6.4 ± 0.8 , 3) as long as snout-vent length in females and 4.9–6.3% (5.5 ± 0.6 , 4) as long in males. Head length accounts for 2.1–2.6% (2.4 ± 0.3 , 3) of snout-vent length in females and 2.1–2.4% (2.2 ± 0.1 , 4) in males. The distance from the anterior border of the eye to the center of the nostril accounts for 15–22% (19 ± 3 , 6) of head-length.

In our sample, cephalic squamation exhibits little variation. All specimens have 2/2 postoculars, 1–1/1–1 temporals, and 7/7 supralabials and infralabials with supralabials 3–4 entering the orbit. AMNH 22277 has two preoculars on one side, all other specimens have single preoculars. The prefrontals do not contact the supralabials. The supraoculars are 71–86% (79 ± 6 , 7) as wide as the frontal. The first three (50% of the time, 7) or the first four infralabials contact the first pair of chinshields so that the third and fourth or just the fourth contact the second. Three to five (3.9 ± 0.7 , 7) gulars and preventrals separate the chinshields from the 214–221 (218 ± 4 , 3) ventrals and 21–22 (21.3 ± 0.6 , 3) subcaudals in females and 213–221 (217 ± 4 , 4) ventrals and 19–24 (21.5 ± 2.4 , 4) subcaudals in males.

The dorsal head scales of this species are mostly black with red and yellow borders. At least, the first five supralabials bear black posterior edges. The infralabials are invariably patterned, usually with black blotches on the third and fourth infralabial. The mental is immaculate or blotched. The nuchal ring extends for two to three vertebrae behind the parietals and extends ventrally as a complete gular band in all specimens except USNM 280426.

In Bolivia, this species has 5.33–7.67 (6.76 ± 0.81 , 7) triads on the body and 0.67–1.33 triads on the tail. Not included in these counts is the incomplete triad (one-third) on the neck. Ventrally, the black rings are as long as or longer than they are dorsally. Where they traverse the vent, black rings may be incomplete ventrally. The first black ring on the neck does not project forward and has a near-vertical anterior margin. The red rings are immaculate or have reduced black apices, and the yellow rings have heavy black apices.

At midbody, the red ring extends for 4–11.5 (8.2 ± 3.0 , 7), the exterior black ring for 3–5 (4.0 ± 0.7 , 7), the yellow ring for 4–8 (5.3 ± 1.3 , 7), and the middle black ring for 2–4.5 (3.4 ± 0.9 , 7) vertebrae. Relative lengths of the rings overlap, although the red ring is usually longest followed in size by the yellow ring, then the exterior black rings. The exterior black rings are 100–133% (120 ± 18 , 7) and the yellow rings 122–200% (160 ± 37 , 7) as long as the middle black ring. The middle black ring is 26–75% (46 ± 17 , 7) as long as the red ring.

Distribution and Comparative Material.—**BOLIVIA.** BENI. Vaca Diez: Riberalta (UMMZ 63820), Tumi Chucua (USNM 280426), Guayaramerin (USNM 280976). **Unknown:** “Rio Itenez, Puerto Capitan Vasquez,” (AMNH 113603). **SANTA CRUZ.** Velasco: Santa Cruz: “Huanchaca I”, Mesa of the Serranía de Huanchaca (NK 604), “Arriba de Lago Caiman, la meseta de Parque Noel Kempff” (NK 1310).

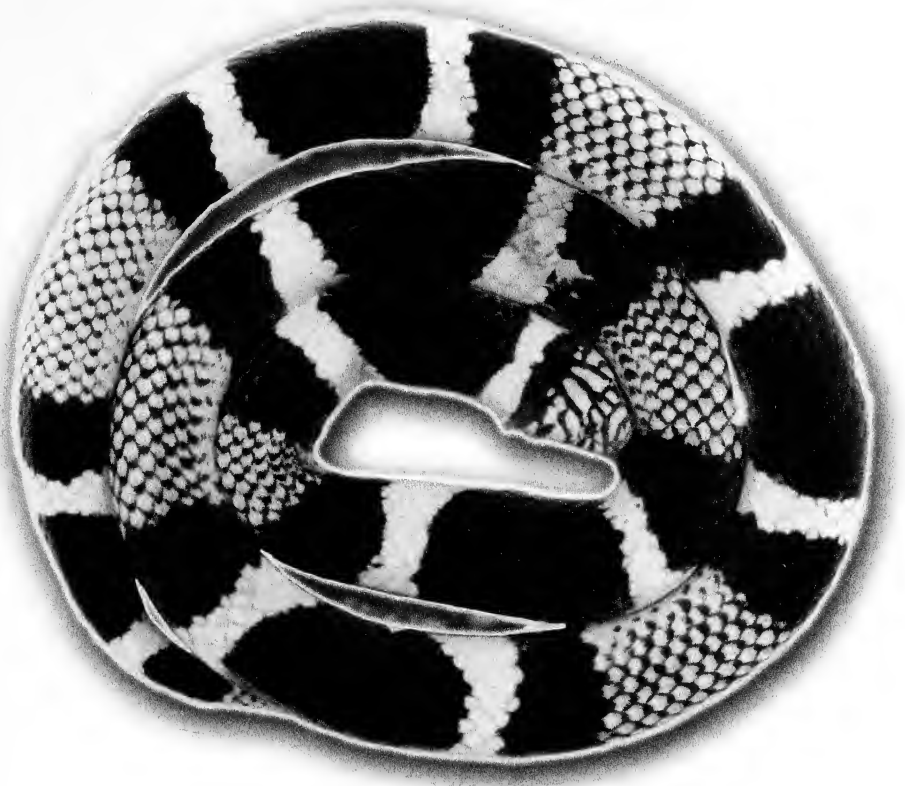


Fig. 14.—*Micrurus surinamensis* (KU 183492 F, SVL 664 mm) from 15 km SW of Villa Tunari, Chapare, Cochabamba.

BRAZIL. PARA: USNM 267833. **BRAZIL. BAHIA:** AMNH 22277.

Micrurus surinamensis Cuvier
(Fig. 14)

Elaps surinamensis Cuvier, 1817:84. SYNTYPES a male (MNHN 3926) and a female (MNHN 3925) [Roux-Esteve (1983) points out that MNHN 3924 is the specimen illustrated by Jan and Sordelli, however this specimen is not a type specimen. Schmidt (1952:29) designated MNHN "4629" (=3926), as a lectotype.]. Cope, 1876:182; Boulenger, 1896:414.

Micrurus surinamensis (Cuvier): Amaral, 1925:17; Amaral, 1948a:38; Amaral, 1948b:159; Fugler, 1986:58; Fugler and Cabot, 1995:60.

Micrurus surinamensis surinamensis (Cuvier): Schmidt, 1952:29; 1955:349; Roze, 1955:491; Peters, 1960:532; Roze, 1967:49; Brongersma, 1967:73, 75; Roze, 1970:219; Hoge and Romano, 1973: 130; Cunha and Nascimento, 1982:23; Carrillo de Espinoza, 1983:45; Dixon and Soini, 1986: 146; Vanzolini, 1986:24; Campbell and Lamar, 1989:152; Golay et al., 1993:183; Jorge da Silva, 1993:74; Carrillo de Espinoza and Icochea, 1995:19; David and Ineich, 1999:155.

Diagnosis.—(1) Dorsal pattern of white, red, and black triads; (2) hemipenis relatively short; tail 10–14% of snout-vent length; (3) one supralabial entering orbit; (4) mental usually separated from chinshields by medial contact of first pair

of infralabials; (5) anal scale usually divided; (6) first triad complete (7) first black ring short and overlapping or closely approximating parietals; (8) dorsal surface of head red with all scales edged in black; (9) extent of black pigment in red and white rings variable; (10) white rings longest ventrally, never constricted or broken ventrally by black rings; (11) scales of chin red with black edges; (12) 5.33–6.67 triads on body, 1–2 triads on tail.

Description.—(Based on 8 females, 7 males, and 2 unsexed specimens). Although one of the most recognizable coralsnakes, relatively few Bolivian specimens have been examined previously. In his review of this species, Schmidt (1952) had access to only two Bolivian specimens, both male. In our sample, extreme total lengths are 1338 mm (a female, NK 723) and 282 mm (a male, CBF 675). The tail is 10–13% (12.1 ± 2.0 , 7) as long as the body in females and 13–14% (13.7 ± 0.4 , 6) as long in males. Head length accounts for 2.4–3.9% (3.1 ± 0.6 , 5) of snout-vent length in females and 2.8–4.3% (3.4 ± 0.6 , 6) in males. Distance from the anterior border of the orbit to the center of the nostril is 17.5–24.6% (22.2 ± 2.9 , 13) of head length.

As for populations elsewhere, Bolivian specimens have a narrow frontal which is 73–92% (83 ± 7 , 11) as wide as the supraocular. KU 183492 has only 6/6 supralabial and supralabial 3/3 enters the orbit. In all other specimens, the fourth supralabial enters the orbit and seven supralabials are present. The prefrontal does not contact the supralabials. Most specimens had two postoculars; one is present on both sides in CBF 949 and on one side only in CBF 868 (9.4%). The Bolivian specimens have 1+1 (81%, 18) or 1+2 (19%, 18) temporals. All specimens had 7/7 infralabials, the first three (9%, 19) or four (91%, 19) contacting the first pair of chinshields. The mental does not contact the chinshields. Three to six (4 ± 1 , 17) gulars and prefrontals separate the second pair of chinshields from 168–182 (179 ± 5 , 8) ventrals and 28–34 (30 ± 2 , 7) subcaudals in females and 165–174 (169 ± 3 , 7) ventrals and 28–36 (34 ± 3 , 7) subcaudals in males. Forty-three percent (15) of the specimens had 2–5 entire subcaudals located proximally on the tail.

In our sample, the first black ring is short and usually covers the posterior tips of the parietals and one to two vertebrae. In CBF 868, the first black ring does not involve the parietals: their tips and 1/2 of the first vertebral are red. Based on 17 males and 13 females, Hoge (1958) concluded that the first ring of the neck triad is complete in males (i.e., a complete gular ring is present) and incomplete in females. However, sexual dimorphism in this character was not evident in our sample. The gular ring includes gulars and the apices of the posterior chinshields. In males and females, the gular ring usually is complete, but in both sexes the scales within the ring are approximately one-half red with black edges. In only three males (e.g., NK 2033), the scales within the ring are entirely black. The second black ring is incomplete in 36% of the specimens and is not sexually dimorphic. In addition to the neck triad, females in our sample have five and two-thirds to six and one-third triads on the body and one to one and two-thirds on the tail. In addition to the neck triad, males have 5.33 to 6.67 triads on the body and one and one-third to two triads on the tail. The rings of this species are sharply angled so that the black rings are longest dorsally and the white rings are longest ventrally. CBF 1763 has an anomalous pattern with black rings that are incomplete ventrally and appear as black circles surrounded by white.

At midbody, the red rings are 6–12 (7.9 ± 2.0 , 15), the exterior black rings are 2–4 (3.1 ± 0.5 , 15), the white rings are 1–2 (1.6 ± 0.4 , 15), and the middle

black rings are 7–10.5 (8.2 ± 1.0 , 15) vertebrals long. Based primarily on material from outside Bolivia, this species has been characterized as having red rings usually longer than middle black rings (Roze, 1996). However, in our sample, this is true for only five specimens. The middle black ring is 67–154% (111 ± 28 , 15) as long as the red ring. The middle black ring is always longer than the exterior black rings and the white rings: the exterior black ring is 33–47% (39 ± 8 , 15) as long and the white ring is 11–31% (20 ± 6 , 15) as long as the middle black ring.

Distribution.—**BOLIVIA. BENI. Gral. José Ballivián:** Estación Biológica del Beni (CBF 1175), “proximo al Estación Biológica del Beni,” (CBF 1763), Bosque Chimanes (CBF 1123). **Moxos:** “carreterra entre el Río Cuberene y el Río Museruna (CBF 1534), San Ignacio de Moxos (NK 2033). **Vaca Diez:** “Río Marmoré, Isla Nicolas Suárez (between Guayaramerin, Bolivia and Guajará-Mirim, Brazil)” (AMNH 113604), Río Marmoré, Guayaramerin (AMNH 113605). **Yacuma:** Estación Biológica del Beni, Campamento El Trapiche (CBF 948). **COCHABAMBA: Chapare.** 15 km SW Villa Tunari, 660 m (KU 183492). **PANDO. Manuripi:** 8 km SW of Santa Rosa (CBF 868). **SANTA CRUZ. Andrés Ibáñez:** Santa Cruz de la Sierra (CM 2795), Terevinto (NK 484), Potrerillo de Guendá (NK 723, NK 1418). **Ichilo:** Buena Vista (NK 838), (Parque Nacional Amboró, $17^{\circ}24'12''$ S, $64^{\circ}14'23''$ W (NK 1324). **Velasco:** Los Fierros, Parque Nacional “Noel Kempff Mercado” (NK 279). **Unknown:** “112 km N Santa Cruz de la Sierra, ca 1200 ft” (AMNH 119936).

Not examined: BMNH 27-8-1-218 (from Buena Vista, Ichilo province, see Schmidt, 1952).

DISCUSSION

The ranges of three coralsnakes approach Bolivia's borders, and each may occur within the country. *Micrurus albicinctus*, *M. mipartitus*, and *M. paraensis* occur in Rondônia (Vanzolini, 1986; Nascimento et al., 1988; Jorge da Silva, 1993). Campbell and Lamar (1989) predict that *M. langsdorffi* probably occurs in Bolivia, however these authors are referring to *M. albicinctus*. Campbell and Lamar (1989) agreed with Cunha and Nascimento's (1982) synonymization of *M. albicinctus* with *M. ornatissimus*, which they considered to be a subspecies of *M. langsdorffi*. Other species of the *M. frontalis* complex may be discovered in Bolivia. Recent collections in the vicinity of the Serranía de Huanchaca have failed to produce a species of this complex other than *M. diana*. In Chiquitos province, *M. diana* occurs in sympatry with *M. pyrrhocryptus*, however the Serranía de Huanchaca lies between the ranges of *M. pyrrhocryptus* and *M. frontalis*. Several Brazilian species such as *Hoplocercus spinosus* just enter the country in this area (Harvey, 1998), and the same may be true for *M. frontalis*: its closest locality is in Mato Grosso (Jorge da Silva and Sites, 1999). *Micrurus baliocoryphus* occurs in the Argentine Mesopotamia and approaches Bolivia in the Paraguayan province of Presidente Hayes (Jorge da Silva and Sites, 1999), however the closest localities are still almost 500 km from the Bolivian border.

A specimen identified as *Micrurus corallinus* (CM 261) by Griffin (1916) and Amaral (1926a) was collected by T. LeBoutelier from “Sierras of Bolivia.” The specimen was missing from the collection during an inventory in August 22, 1960, and the specimen has not yet been found. Griffin (1916) reported that LeBoutelier rarely provided accurate locality data; many specimens he collected bear no data other than from “South America.” Reporting on the specimen at the Carnegie Museum, he gave “LeBoutelier Collection, South America,” apparently placing little faith that the specimens actually came from Bolivia. Amaral (1926a) reported this species from Bolivia. The specimen was a female 597 mm total length (tail 83 mm) with “1,1” temporals, a divided anal, 200 ventrals, 43 divided subcau-

dals, 16 black rings on the body, and 6 black rings on the tail (Amaral, 1926a; Griffin, 1916). However, both authors' concept of *M. corallinus* was flawed; in a later publication, Amaral (1930a) thought that *Elaps balzani* Boulenger (= *M. annellatus*) was *M. corallinus corallinus*. Currently, *Micrurus corallinus* is thought to be restricted to southeastern and central Brazil, eastern Paraguay, and northeastern Misiones, Argentina (Campbell and Lamar, 1989; Roze, 1996).

Fugler (1986) included *Micrurus ibiboboca* (Merrem) in the Bolivian fauna citing Boulenger (1898) and Werner (1901). In his literature cited, Fugler lists two publications of Boulenger for 1898. Neither publication contains a reference to *M. ibiboboca*. One of these publications reports on a collection from the upper Río Paraguay (Boulenger, 1898b) and contains a specimen of the *Micrurus frontalis* complex. However, Fugler clearly was referring to Boulenger's report on Balzan's collection (Boulenger, 1898a), where Boulenger lists "*Elaps marcgravii*, Wied." from Reyes and Santa Ana de Movimas, Beni. Fugler is correct that *E. marcgravii* is a synonym of *M. ibiboboca*, however, Boulenger applied the name to *M. lemniscatus* as well (Schmidt, 1957). Other authors have applied the name to *M. spixii* and *M. obscurus*, however Boulenger used Peters' junior synonym *Elaps heterozonus* to refer to *M. obscurus*. *Micrurus ibiboboca* is restricted to eastern Brazil and the western limit of its range is far from the Bolivian border.

Schmidt (1936) pointed out the "difficult problems of distribution" posed by a specimen of *Micrurus tschudii* said to be from Bolivia in the Museum National d'Histoire Naturelle in Paris, whereas all other specimens of *M. tschudii* are from coastal Peru. He chose not to include Bolivia in the distribution of this species. Less skeptically, Roze (1967, 1983, 1996) reports that the subspecies *M. tschudii tschudii* occurs on the "Pacific slopes from southern Ecuador to southern Peru and probably northwestern Bolivia" (Roze, 1983). Without comment, Bolivia was included in the distribution of this species by Peters and Orejas-Miranda (1970) and repeated by Fugler and Cabot (1995). Campbell and Lamar (1989) cautioned "the postulated occurrence of *M. tschudii* in Bolivia is difficult to explain, as the Andes constitute a formidable barrier to dispersal in this region."

The specimen of *Micrurus tschudii* collected by Wiener and labelled "Bolivia" may well have come from northern Chile or southwestern Peru. These coastal regions were inside the border of Bolivia prior to Bolivia's war with these countries between 1879 and 1884. Nonetheless, the most southern localities for this species are in Lima Department (Carrillo de Espinoza and Icochea, 1995). Schmidt (1936) remarked that the specimen said to come from Bolivia more closely agreed with his diagnosis of *Micrurus tschudii olssoni* except that it lacks a mottled snout.

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TAXONOMIC STATUS OF *THELEGNATHUS BROWNI* BROOM, A PROCOLOPHONID REPTILE FROM THE SOUTH AFRICAN TRIASSIC

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ABSTRACT

The holotype of the procolophonid reptile *Thelegnathus browni*, from the Early-to-Middle Triassic *Cynognathus* Assemblage Zone of the Beaufort Group, South Africa, consists of an isolated left maxilla that was originally described by Robert Broom early last century. This specimen is redescribed and compared with maxillae of more recently described procolophonid taxa from Eastern Europe and North America. A single apomorphy, the presence of marginal teeth that increase in mesiodistal diameter posteriorly, was proposed to diagnose the genus *Thelegnathus*. However, this character is present also in several Laurasian procolophonid genera. The specific diagnostic features of *T. browni* are either plesiomorphic for procolophonids or are of doubtful taxonomic value. Accordingly, *T. browni* is declared a nomen dubium, and the four species from the *Cynognathus* Assemblage Zone recently assigned to *Thelegnathus* are transferred to new genera. The following replacement names are proposed for these species: *Thelerpeton* gen. nov., for *T. oppressus*; *Theledectes* gen. nov., for *T. perforatus*; *Thelephon* gen. nov., for *T. contritus*; and *Teratophon* gen. nov., for *T. spinigenis*. These taxonomic revisions suggest that there is no basis for a hypothesis that postulates an endemic radiation of procolophonids in central Gondwana (by species of *Thelegnathus*), and indicate that the genus *Thelegnathus* has no utility in biostratigraphic concepts for the Beaufort Group.

KEY WORDS: Procolophonidae (*Thelegnathus*), Reptilia, Triassic, Beaufort Group, South Africa

INTRODUCTION

In the first half of the last century, Robert Broom described a plethora of new synapsids and reptiles from the Permo-Triassic Beaufort Group of the Karoo Basin, South Africa. Most of his new taxa were created for single skulls, but many were based on isolated elements. Among the latter is the maxilla of a small Triassic reptile discovered by Alfred “Gogga” Brown in *Cynognathus* Assemblage Zone strata near Aliwal North (southern Karoo Basin), and subsequently described by Broom (1905) as the new genus and species *Thelegnathus browni*. However, as with many of Brown’s discoveries, the precise locality where the specimen was found remains unknown. Broom (1936) later assigned an isolated maxilla and a dentary to *Thelegnathus* (both specimens are now lost: S. Kaal, personal communication), but more complete specimens would not be attributed to the genus for another four decades (Gow, 1977).

Broom (1936) distinguished *Thelegnathus browni* from other procolophonids by tooth morphology: he noted that the teeth of the holotype became progressively greater in mesiodistal diameter towards the posterior of the tooth row. This character was recognized as diagnostic at the generic level by Gow (1977). The curvature of the occlusal plane of the teeth and the nature of the wear on the teeth

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were regarded by Gow (1977) as diagnostic at the specific level. There are problems with these diagnostic characters because the holotypic tooth row is damaged posteriorly, and it is unclear if an additional tooth was present. In addition, a number of European and North American procolophonid taxa, unknown during Broom's (1905, 1936) era but known by the time Gow (1977) published his reappraisal, display tooth morphologies and wear reminiscent of the holotype of *Thelegnathus browni*.

Gow (1977) assigned four new species, also from the *Cynognathus* Assemblage Zone in the southern Karoo Basin, to the genus *Thelegnathus*, thereby more than doubling the number of procolophonid species known from that biozone. Gow's (1977) systematic work implies that there was a small, localized radiation of procolophonids in the Karoo Basin in the Early to Middle Triassic. Ivakhnenko (1983), however, expressed doubt that additional species should be assigned to *Thelegnathus*. Ivakhnenko's view was reiterated, in part, by Novikov (1991), who thought that only one of Gow's (1977) species (*T. contritus*) was correctly assigned to *Thelegnathus*.

The recognition of five species of *Thelegnathus* in the *Cynognathus* Assemblage Zone inevitably led to the recognition of a stratigraphic range for the genus (Kitching, 1995). Accordingly, it is possible that *Thelegnathus* may come to play a role in biostratigraphic considerations of that biozone, as has the genus *Procolophon* for the underlying *Lystrosaurus* Assemblage Zone (Groenewald and Kitching, 1995; Neveling et al., 1999). In order to examine monophyly of the genus *Thelegnathus*, and so to assess its potential stratigraphic utility, we reexamined the holotype of *Thelegnathus browni* and compared it to a broad range of procolophonid taxa.

Institutional abbreviations used in this paper: BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; SAM, South African Museum, Cape Town.

SYSTEMATIC PALEONTOLOGY

Reptilia Laurenti, 1768

Parareptilia Olson, 1947

Procolophonia Seeley, 1888

Procolophonidae Lydekker, 1890

Thelegnathus browni Broom, 1905

Holotype.—SAM PK-5869, an isolated left maxilla (Figure 1) preserved in breccia.

Locality and Horizon.—An unknown locality in the Aliwal North District, Eastern Cape Province, South Africa; *Cynognathus* Assemblage Zone, Beaufort Group, Lower or Middle Triassic.

Diagnosis.—Taxon is a nomen dubium.

Description

The holotype has a quadrangular outline in lateral view (Fig. 1A), but the bone is damaged posteriorly and it seems likely, judging from the morphology seen in *Procolophon* (Carroll and Lindsay, 1985) and *Tichvinskia* (Ivakhnenko, 1973), that an anteroposteriorly short edentulous portion has been lost. The maxilla is thickest ventrally and the lateral surface appears to slope gradually towards the dorsal tip.

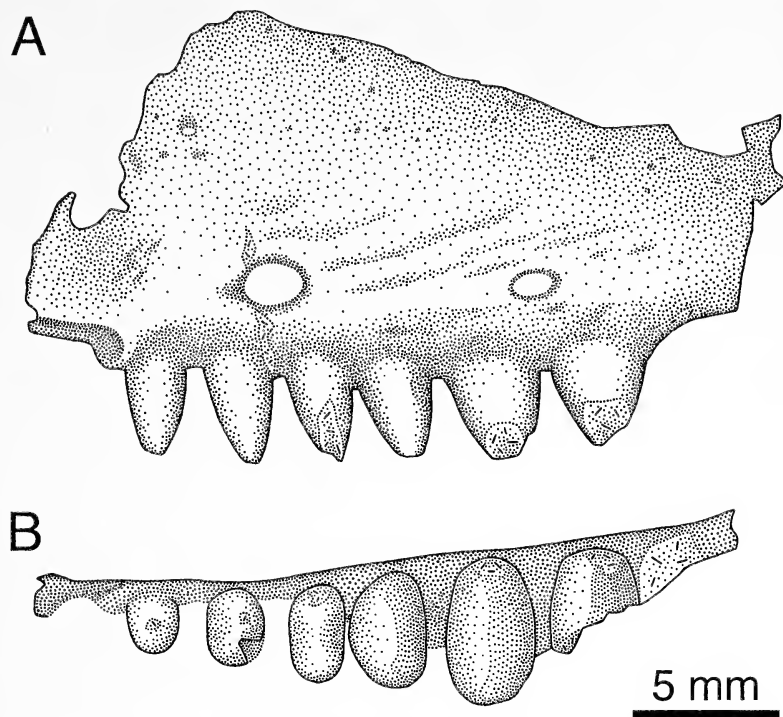


Fig. 1.—*Thelegnathus browni* Broom, holotype SAM PK-5869, left maxilla. A. Lateral view. B. Occlusal view.

The lateral surface is pierced by two large openings, by a smaller opening, and by many fine pits. The largest opening lies just dorsal to the second and third teeth. Judging from its topographical relationships to the ventral margin and the sutural surface for the premaxilla, this opening is the anterolateral foramen (Laurin and Reisz, 1995). It gives rise to a shallow, rapidly attenuating channel that extends anteriorly from the opening. The smaller, posterior opening appears to be a supralabial foramen. It lies in the same approximate position of single or paired foramina that have been illustrated for *Procolophon* (Carroll and Lindsay, 1985) and other procolophonoids (e.g., Modesto et al., 2001). The smallest opening lies dorsal and slightly anterior to the anterolateral foramen, and appears to be a minor nutrient foramen. Tiny pits are positioned diffusely across the dorsal part of the lateral surface.

A series of long, shallow grooves ornament the ventral half of the lateral surface (Fig. 1A). The grooves nearest the ventral margin are anteroposteriorly short and dorsoventrally narrow, but they become longer and broader dorsally and eventually become confluent with the lateral surface. At approximately the same height but at the anterior end of the bone there is a shallow, circular fossa on the lateral surface of the maxilla. This fossa, because it lies directly dorsal to the sutural surface for the premaxilla, appears to be a very shallow version of the maxillary depression seen in *Procolophon*, *Tichvinskia*, and *Contritosaurus* (Ivakhnenko, 1973, 1974; Carroll and Lindsay, 1985). None of the skulls described by Gow (1977) feature a maxillary depression.

Six teeth are present. Broom (1936) mentioned the possibility of a seventh tooth, but the ventral surface of the maxilla immediately posterior to the sixth tooth is too damaged to make this determination (Fig. 1B). If a seventh tooth was indeed present, it must have been a small tooth, because the ventral margin of the maxilla slopes upwards immediately posterior to the last preserved tooth (Fig. 1A), and there does not appear to be room for a tooth the size of the posterior two or three teeth. As described by Gow (1977), the teeth increase in both mesiodistal and labiolingual diameter from anterior to posterior. The first tooth is subconical, whereas the succeeding teeth have labial and lingual cusps that resemble those illustrated for *Tichvinskia* and *Macrophon* (Ivakhnenko, 1975: fig. 1). Wear is present on each of the last three teeth as a transverse, crescentic facet running from cusp to cusp on the posterior half of the tooth apex.

Discussion

Thelegnathus browni was distinguished from other procolophonids by Broom (1936) by maxillary teeth that become larger from anterior to posterior in the series. Gow (1977) regarded this characteristic as diagnostic at the generic level. However, it works as a diagnostic character only if comparisons are restricted to the South African procolophonoid genera *Owenetta* and *Procolophon*. If the holotype of *T. browni* is missing a seventh tooth that is smaller than the preceding tooth, then again the diagnosis does not work because *Myocephalus crassidens* (Broom, 1936), also from the *Cynognathus* Assemblage Zone of South Africa, has, except for the posteriormost tooth that is the smallest of the upper dentition, maxillary teeth that increase in size from anterior to posterior. It seems unlikely that *Myocephalus* is a junior synonym of *Thelegnathus*, because the maxillary morphology of the former genus (Modesto, personal observation) is strongly reminiscent of the maxillary morphology of leptopleuronine procolophonids (e.g., Sues et al., 2000), whereas that of *T. browni* is not (Fig. 1).

There are also a number of Laurasian procolophonoid taxa whose teeth can be described as growing larger from the front to the back of the marginal dentition. The molariform teeth of *Kapes amaenus* (Ivakhnenko, 1975), *Samaria concinna* (Novikov, 1991), *Acadiella psalidodon*, *Haligonia bolodon*, and *Scoloparia glyphanondon* (Sues and Baird, 1998) all exhibit a progressive increase in size to the posterior end of the tooth row. It is becoming clear that the phenomenon of marginal teeth that become larger from anterior to posterior in a tooth series is typical of many procolophonid taxa. It may be that this character diagnoses a clade of procolophonids that includes not only *T. browni* and the species described and assigned by Gow (1977) to the genus *Thelegnathus*, but also one that includes other procolophonids that have been described in recent years from both Europe and North America. The most appropriate test of this idea would be a phylogenetic analysis of a variety of procolophonoid taxa in order to see if some or all of the taxa that are characterized by this particular dental phenomenon form a natural group. However, it is ironic that many, if not most, of the taxa that do feature such a dentition are known from very fragmentary remains (partial jaws), and it therefore seems unlikely that parsimony analysis would result in the discovery of only a few (or less) minimum-length trees.

The fragmentary nature of the holotype of *Thelegnathus browni* itself leaves little clues about the affinities of the taxon within Procolophonidae and of the putative monophyly of the genus *Thelegnathus*. Apart from the nature of the

dentition discussed above, the morphology of the holotype is unlike that of the maxillae of the other four species (Gow, 1977) in the presence of a maxillary depression and of ornamentation comprising shallow grooves. The former feature is plesiomorphic for procolophonids because it is seen in *Procolophon trigoniceps* (Carroll and Lindsay, 1985) as well as the more basal procolophonoid *Coletta seca* (Modesto et al., 2002). Therefore, the absence of this fossa in the four species described by Gow (1977) is suggestive of two possibilities: (1) that *T. browni* is the basalmost member of a clade that includes the other four species of *Thelegnathus*, or (2) that these other four species are more closely related to other procolophonids that are also characterized by the loss of the maxillary depression, such as *Hypsognathus* (Sues et al., 2000), than they are to *T. browni*. The “curve of the occlusal plane” and “nature of tooth wear” were thought to be diagnostic for *T. browni* (Gow, 1977), but the former is seen also in *Procolophon* (Carroll and Lindsay, 1985: fig. 5) and *Hypsognathus* (Sues et al., 2000: fig. 2f), and thus is probably symplesiomorphic for procolophonids. The diagnostic utility of tooth wear is debatable given that similar wear is seen in *Tichvinskia* and *Macrophon* (Ivakhnenko, 1975). The presence of shallow grooves on the lateral surface of the maxilla may be an autapomorphy of *T. browni*, as they have not been described in other taxa to our knowledge. However, taking into consideration the small size of many procolophonid specimens and the grinding methods that have been used to prepare some materials, particularly those from South Africa, it is unclear if this kind of ornamentation is more widespread and was unintentionally removed from known materials. It is uncertain even if the presence of such shallow grooves on the external surface of a dermal roofing element is a useful phylogenetic character.

The paucity of phylogenetic information that is offered by SAM PK-5869, the holotype of *Thelegnathus browni*, allows little choice but to regard *T. browni* as a nomen dubium. With *T. browni* a nomen dubium, assignment of additional species to the genus becomes unwarranted. Accordingly, the four species that were assigned to *Thelegnathus* by Gow (1977) require a new generic name. However, because there is no evidence that any of Gow's species are congeneric, we assign a new genus to each species. The authors intend to conduct anatomical reappraisals of all four species in the near future in order to place these species in the context of procolophonoid phylogeny. The systematic paleontology of the four species is as follows:

SYSTEMATIC PALEONTOLOGY

Procolophonidae Lydekker, 1890

Thelerpeton oppressus (Gow) gen. nov.

Etymology.—The replacement genus name is from the Greek words *thele* and *herpeton*, which mean “nipple” and “creeper” (or “crawler”), respectively, and is inspired by Broom's (1905) nomen *Thelegnathus*, which means “nipple jaw”.

Holotype.—BP/1/4538 (formerly “BPI 155”), a skull with poor surface detail (Figure 2).

Locality and Horizon.—The farm Hugoskop in Rouxville District, Free State Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic. The localities from which all of Gow's (1977) specimens were recovered also yielded specimens of the dicynodont genus *Kannemeyeria* (Kitching, 1977), now recognized as an index taxon for the middle part (Subzone B)

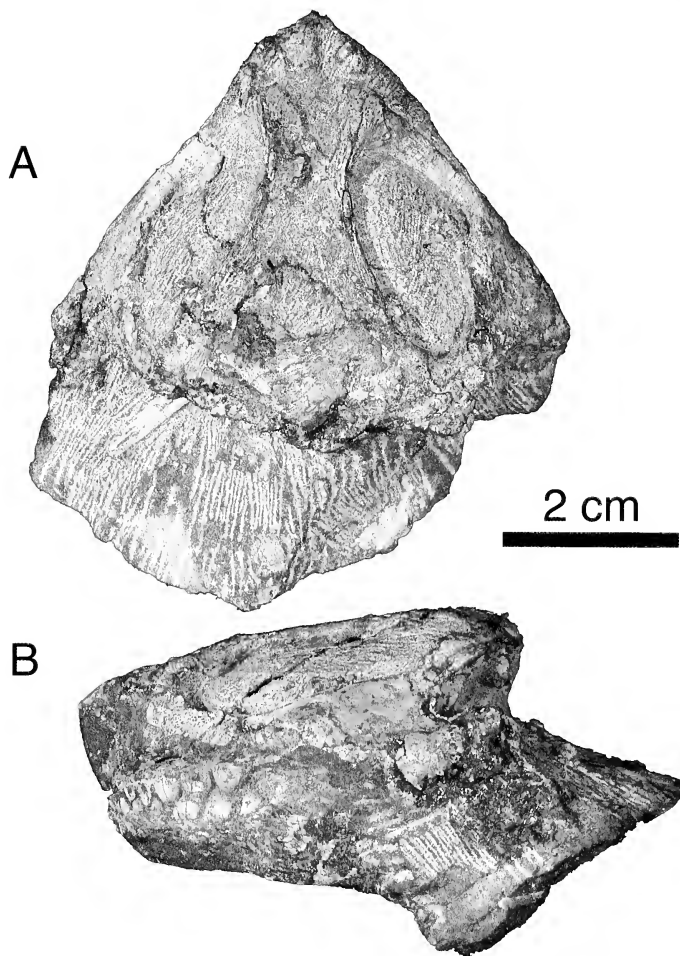


Fig. 2.—*Thelerpeton oppressus* (Gow) gen. nov., holotype BP/1/4538. A. Dorsal view of skull. B. Left lateral view of skull and mandible.

of the *Cynognathus* Assemblage Zone, which is Anisian in age (Hancox et al., 1995).

Diagnosis.—A procolophonid reptile with bulbous marginal teeth “with the crowns pinched up to present a small occlusal area (Gow, 1977, p. 112)”, and dentary dentition that is undercut labially by a continuous, longitudinal sulcus.

Comments.—Bulbous teeth with narrow (“pinched”) apices are present also in the Eastern European genera *Kapes* (Ivakhnenko, 1975) and *Samaria* (= *Orenburgia*; Novikov, 1991), which may be suggestive of close relationships among these taxa. The labial sulcus that undercuts the dentary teeth of *Thelerpeton* is reminiscent of the sulci described for *Contritosaurus* (Ivakhnenko, 1974), but the condition in the latter does not seem to be as developed as that seen in the former taxon. The great posterior expansion of the orbits (past the posteriormost point of the pineal opening) in the holotype suggests that *Thelerpeton oppressus* is a leptopleuronine procolophonid. The dentition of the paratypes, BP/1/4584 and BP/1/4586, differs from that of the holotype in lacking the labial sulcus and being

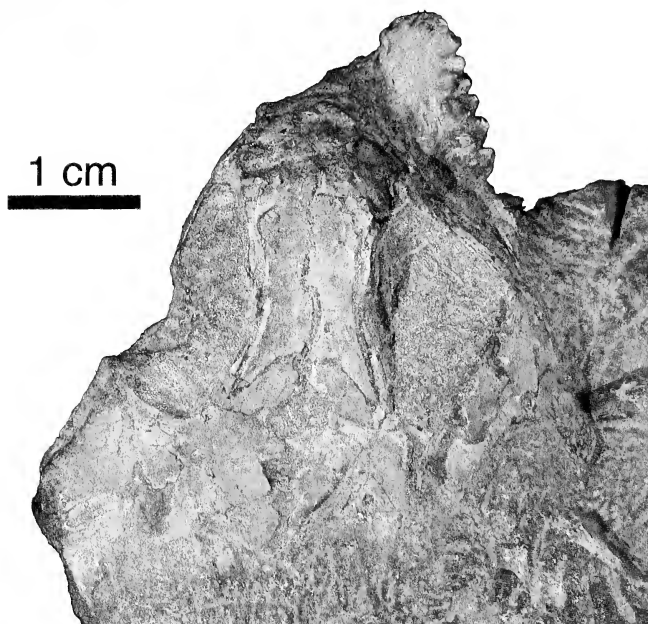


Fig. 3.—*Theledectes perforatus* (Gow) gen. nov., holotype BP/1/4585, skull and right mandibular ramus in dorsal view.

deeply inset from the labial surface. They share the latter feature with the second species described by Gow (1977), *T. perforatus*, the holotype and only known specimen of that species, which is known from the same locality (Hugoskop) as *T. oppressus*. However, there are differences in the dentition, particularly the absence of the autapomorphy of *T. perforatus* (see below), which suggest that BP/1/4584 and BP/1/4586 do not belong to that species.

Theledectes perforatus (Gow) gen. nov.

Etymology.—The replacement genus is derived from the Greek words *thele* and *dektes*, the latter meaning “biter”, which is an oblique reference to the multiple rows of teeth that characterize the taxon. The prefix is inspired by *Thelegnathus* Broom (1905).

Holotype.—BP/1/4585, a dorsoventrally compressed, partial skull (Figure 3).

Locality and Horizon.—The farm Hugoskop in Rouxville District, Free State Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic (Anisian).

Diagnosis.—A procolophonid reptile distinguished from all other parareptiles by the presence of multiple rows of marginal teeth.

Comments.—This species is the sole parareptile with multiple rows of marginal teeth. The only other early reptiles known to have multiple rows of teeth are rhynchosaurs (e.g., Dilkes, 1998) and some captorhinids (e.g., Dodick and Modesto, 1995; Modesto, 1998). The presence of only two incisiform dentary teeth suggests that *Theledectes perforatus* is a basal leptopleuronine, as the same number is found in *Scoloparia glyphanodon* (Sues and Baird, 1998). Four and three incisiform dentary teeth are present in *Tichvinskia vjatkensis* (Ivakhnenko, 1973) and *Procolophon trigoniceps* (Carroll and Lindsay, 1985), respectively; these two

taxa were identified as basal procolophonids in the phylogenetic analysis of Modesto et al. (2002). The distinctive curvature of the labial excavation associated with the deep inseting of the marginal dentition (Gow, 1977; fig. 4C) is reminiscent of the condition seen *Hypsognathus fenneri* (Sues et al., 2000), an observation suggesting that *Theledectes perforatus* is related more closely than *Thelerpeton oppressus* is to leptopleuronine taxa such as *Hypsognathus fenneri*. The presence of single rows of marginal teeth in the *Thelerpeton* paratypes BP/1/4584 and BP/1/4586 implies that these specimens are not assignable to *Theledectes perforatus*.

Thelephon contritus (Gow) gen. nov.

Etymology.—The generic name is from the Greek word *thele* and *-phon*, the latter being the final syllable of *Procolophon*, and now a common suffix in procolophonid generic names (e.g., *Macrophon*, *Microphon*, *Timanophon*).

Holotype.—BP/1/3512, a partial skull lacking the snout and anterior third of the mandible (Figure 4).

Locality and Horizon.—The farm Winnaarsbaken, Burgersdorp District, Eastern Cape Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic (Anisian).

Diagnosis.—This procolophonid is distinguished from other South African species by the presence of a posterior marginal tooth that is almost twice as expanded mediolaterally as the neighboring teeth.

Comments.—This species has no obvious cranial autapomorphies, and its dentition, which was used to distinguish it from the other species assigned to *Theleognathus* by Gow (1977), resembles in general that of the Laurasian procolophonids *Acadiella psalidodon* and *Halignia bolodon* (Sues and Baird, 1998). The holotype and only known specimen of *Thelephon contritus* does include postcranial material in addition to the skull (Gow, 1977), and it will need to be carefully prepared and redescribed in order to determine if it is a valid species.

Teratophon spinigenis (Gow) gen. nov.

Etymology.—The generic name is from the Greek word *teratos* and *-phon*; the former word means “a wonder” or “monster”, whereas the latter is from *Procolophon*.

Holotype.—BP/1/4299, the nearly complete skull of a large individual (Figure 5).

Locality and Horizon.—The farm Lemoenfontein, Rouxville District, Free State Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic (Anisian).

Diagnosis.—A taxon distinguished from other procolophonids by the presence of a large, posterolaterally-directed spine-like process of the quadratojugal.

Comments.—The quadratojugal process of *Teratophon spinigenis* is like that of *Procolophon trigoniceps* in being a single projection (some leptopleuronines have smaller, multiple spines produced by the quadratojugal), which suggests that *Teratophon* and *Procolophon* are close relatives (Modesto et al., 2002). However, the spine of the former genus is remarkably much larger than that of the latter. Interestingly, the small cheek spine of *Theledectes* resembles that of *Teratophon* in its general morphology, more so than the cheek spine of *Procolophon* (Damiani, personal observation). It is possible that the presence of a single quadratojugal spine, which is considered diagnostic of procolophonines by Modesto et al.

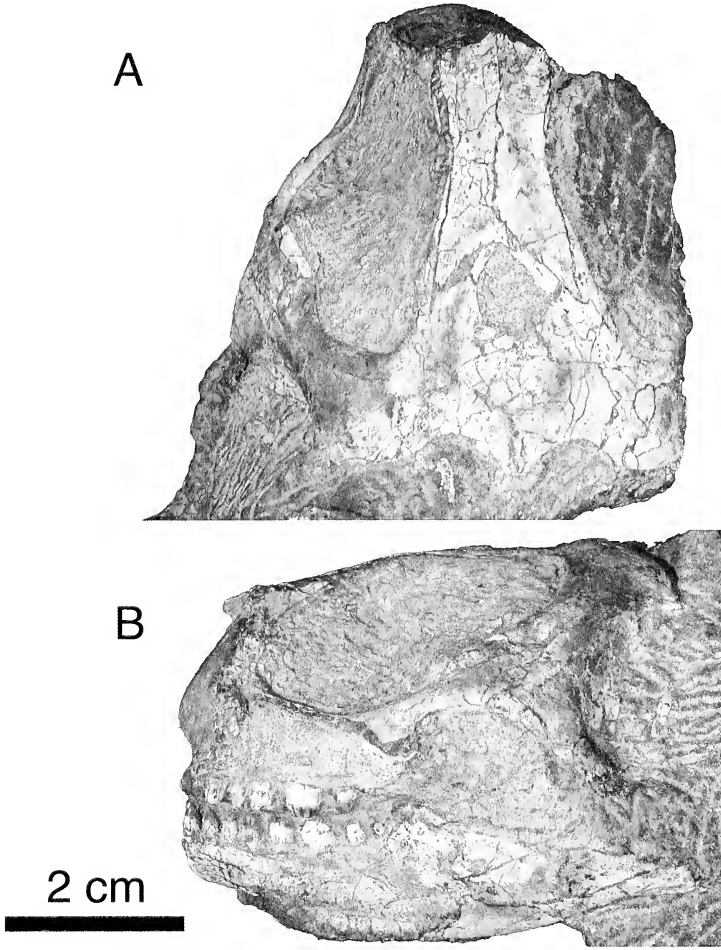


Fig. 4.—*Thelephon contritus* (Gow) gen. nov., holotype BP/1/3512. A. Dorsal view of skull. B. Left lateral view of skull and mandible.

(2002), is instead plesiomorphic with respect to the presence of multiple cheek spines of leptopleuronines.

CONCLUSIONS

The procolophonid *Thelegnathus browni* Broom, known only from a single specimen from the *Cynognathus* Assemblage Zone of the Aliwal North District, South Africa, is a nomen dubium. The sole apomorphy that has been attributed to the genus, the presence of marginal teeth that progressively increase in size towards the posterior end of the tooth row, is shared with a number of Laurasian procolophonids and can no longer be regarded a tenable generic synapomorphy. The four species assigned to the genus by Gow (1977) are, therefore, each assigned a new generic name.

The nomen dubium status of *Thelegnathus browni*, and resultant transfer of *T. oppressus*, *T. perforatus*, *T. contritus*, and *T. spinigenis* to new respective genera,

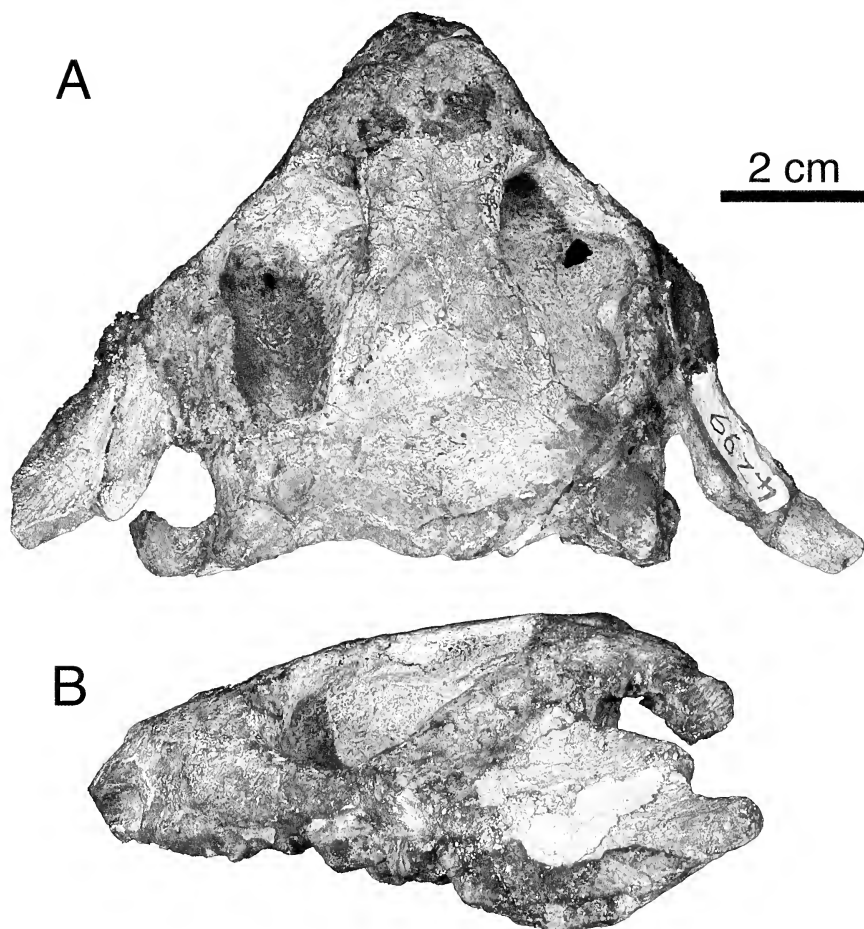


Fig. 5.—*Teratophon spinigenis* (Gow) gen. nov., holotype BP/1/4299, skull. A. Dorsal view. B. Left lateral view.

indicates that *Thelegnathus* has no utility in biostratigraphic considerations of the Beaufort Group. Similarly, the traditional concept of the genus *Thelegnathus* was of a small group of procolophonid species that were endemic to central Gondwana (southern Africa), yet we conclude that there is no compelling evidence for an endemic radiation of procolophonids in the Karoo Basin during the Early to Middle Triassic. Investigations of procolophonid biogeography will be served better by detailed appraisals of the anatomy of all procolophonid taxa and the inclusion of such data into phylogenetic analyses of procolophonid phylogeny. A series of recent studies (Sues and Baird, 1998; Gow, 2000; Spencer, 2000; Sues et al., 2000; Modesto et al., 2001, 2002; Evans, 2001; Reisz and Scott, 2002) suggests that we are undergoing something of a renaissance in procolophonoid research. It is hoped that such work will lead to a better understanding not only of the evolution of these widespread fossil reptiles, but also of the biostratigraphy of the Triassic sediments that preserve them as well.

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EARLY CRETACEOUS FROGS FROM MOROCCO

MARC E. H. JONES¹SUSAN E. EVANS¹DENISE SIGOGNEAU-RUSSELL²

ABSTRACT

The Lower Cretaceous Moroccan locality of Ksar Met-Lili near Anoual has yielded a diverse microvertebrate assemblage including mammals, small reptiles, and amphibians. Here the frogs are described for the first time. Although the material is fragmentary, iliac structure, supplemented by other cranial and postcranial elements, demonstrates the presence of two distinct taxa. One genus is interpreted as a discoglossid, related to members of the Jurassic North American genus *Enneabatrachus*. The second frog represents a new taxon, and is here named *Aygroua anoualensis*. It is more difficult to classify, but attributed procoelous vertebrae and a specialized premaxillary-maxillary overlap suggest it is probably a mesobatrachian, possibly a basal pipimorph.

KEY WORDS: Frogs, Anura, Anoual, Lissamphibia, Cretaceous, Morocco

INTRODUCTION

Frogs and toads (Anura) form a large and successful group of tetrapods, with over 4000 living species distributed globally except for polar areas (Stebbins and Cohen, 1995). Traditionally (e.g., Duellman, 1975), frogs were divided between the Archaeobatrachia (*Ascaphus*, *Leiopelma*, discoglossids, pipoids, and pelobatoids) and the Neobatrachia (all derived frogs including ranids, bufonids, and hylids). However, most more recent authors (e.g., Laurent, 1979; Ford and Cannatella, 1993; Hillis et al., 1993; Henrici, 1994, 1998a,b; Trueb, 1996; but see Hay et al., 1995; Hedges and Maxson, 1993; Gao and Wang, 2001) recognize Mesobatrachia as the sister group of Neobatrachia, with a morphology somewhat intermediate between that of basal frogs and higher taxa (Fig. 1). Mesobatrachian and neobatrachian frogs together form the Pipanura (Ford and Cannatella, 1993). Mesobatrachia (sensu Ford and Cannatella, 1993) includes two major clades—the Pelobatoidea (pelobatids [including megophryines], and pelodytids) and the Pipoidea (rhinophrynids, pipids, and the extinct palaeobatrachids). Within the Pipoidea, pipids and palaeobatrachids are sister taxa (forming the Pipimorpha of Ford and Cannatella, 1993). Gao and Wang (2001) recently proposed a very different arrangement whereby pelobatoids were more closely related to discoglossids and Mesobatrachia was paraphyletic. However, their analysis did not include any neobatrachians. In this paper, we have kept to the more widely accepted phylogeny of Ford and Cannatella (1993).

The fossil history of frogs extends back into the Early Triassic, with the stem salientians *Triadobatrachus* (Madagascar, Rage, and Roček, 1989) and *Czatkobatrachus* (Poland, Evans, and Borsuk-Bialynicka, 1998). There is then a considerable hiatus before the first records of crown-group anurans in the Early Jurassic (*Vieraella*, Argentina, Reig, 1961;

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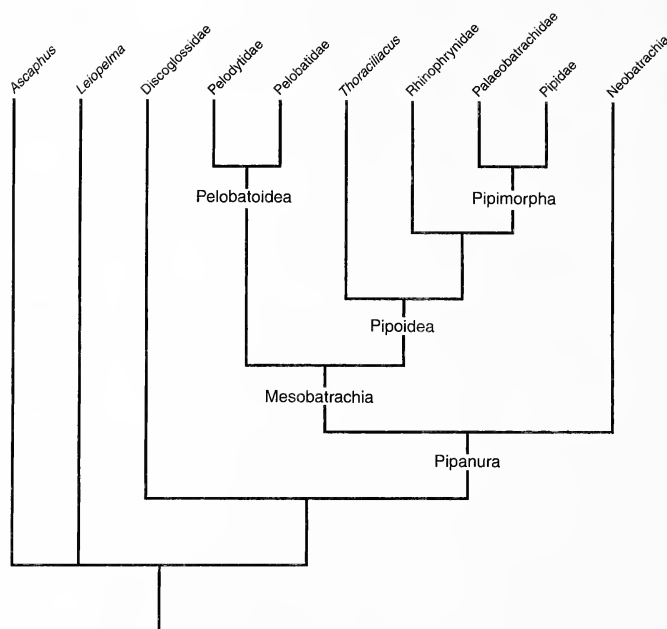


Fig. 1.—Phylogenetic relationships of major anuran groups. The Early Cretaceous genus *Thoraciliacus* has been added since it features in the discussion. Based mainly on Ford and Cannatella, 1993 and Trueb, 1999.

Prosalirus, USA, Shubin and Jenkins, 1995; Jenkins and Shubin, 1998). Discoglossids are first recorded from the Middle Jurassic (Evans et al., 1990), pipoids and pelobatoids from the Late Jurassic (Evans and Milner, 1993; Henrici, 1998*a, b*; Sanchíz, 1998), and neobatrachians from the Late Cretaceous (leptodactylids, Báez and Peri, 1989). However, our knowledge of the Mesozoic record of Gondwana remains limited. In Africa, Mesozoic frogs are extremely rare. Frog remains have been recorded, but not described, from the Early Cretaceous of Cameroon (Congleton, 1988; Flynn and Brunet, 1989) and Malawi (Jacobs et al., 1990), whereas in the Late Cretaceous, pipoids and other frogs are known from Niger (Broin et al., 1974; Báez and Rage, 1998), the Sudan (Werner, 1994; Evans et al., 1996), Madagascar (Asher and Krause, 1998), and South Africa (Haughton, 1931; Estes, 1977).

The Moroccan microvertebrate locality of Ksar Met-Lili (Anoual) is situated in the Eastern High Atlas Mountains, 100 km east of the city of Anoual. This basal Cretaceous outcrop has produced an important and diverse assemblage of mammals (Sigogneau-Russell, 1988, 1991*a, b*, 1992, 1995) as well as other small vertebrates (Sigogneau-Russell et al., 1990, 1998), including sharks (Duffin and Sigogneau-Russell, 1993), lizards (Richter, 1994; Broschinski and Sigogneau-Russell, 1996), two taxa of sphenodontian (Evans and Sigogneau-Russell, 1997), and several amphibians, including albanerpetontids, caecilians (Evans and Sigogneau-Russell, 2001) and the frogs described here.

GEOLOGY AND MATERIAL

The 'couches rouges' of the High Atlas form a continuous sequence from Middle Jurassic (Bathonian) to Lower Cretaceous (Aptian) (Sigogneau-Russell et al., 1990). Microvertebrate material comes from a calcareous lens about 0.2 m thick and covering an area of roughly 200 m². This lens represents a continental deposit intercalated between marine beds, and has been

interpreted as forming part of a deltaic sedimentary environment close to the sea. Analysis of the calcareous nannofossils (holococcoliths) suggests a basal Cretaceous (Berriasian) age for the assemblage as a whole (Sigogneau-Russell et al., 1990; Duffin and Sigogneau-Russell, 1993). Vertebrate remains are small and completely disarticulated. The bones are frequently broken, but appear to have been deposited under relatively quiet conditions since they show little evidence of either polishing or abrasion.

The frog material falls into two distinct morphotypes demonstrating the presence of two discrete taxa. On the basis of comparisons with modern material, the Anoual frogs were relatively small, with a snout-vent length of around 45 mm (35–60 mm). Only a minority of elements represent the upper size range, suggesting that most Anoual frogs were immature at death. This is supported by the weak ossification of all but a few of the vertebral articulations.

METHODOLOGY

Frog bones are highly distinctive in their morphology, and there is little possibility of confusion with the bones of other tetrapods. Anuran osteology has also been comparatively well studied (e.g., Lynch, 1971; Trueb, 1973, 1993). The Anoual frog material consists of around 200 individual fragments representing fifteen different skeletal elements, the most common being presacral vertebrae, maxillae, and ilia. The ilium is generally considered to be the most characteristic and easily recognized anuran element in microvertebrate assemblages (e.g., Sanchíz, 1998), and ilia are frequently used as holotypes. At Anoual, the presence of two distinct iliac morphologies signals the presence of two distinct taxa, a conclusion supported by the recognition of two morphotypes for almost every other skeletal element represented. However, since the Anoual frog material is fragmentary and completely disarticulated, the task of matching skull, vertebral, and limb elements with the individual iliac types is not straightforward, particularly when the two frogs are of similar size, are mostly immature, and may have been present in comparable numbers.

One of the two iliac types closely matches that of basal discoglossid frogs from several Jurassic and Early Cretaceous localities in Europe and North America. The other lacks obvious discoglossid characters and apparently belongs to a different anuran group. In the descriptions that follow, the cranial and postcranial elements that show the closest resemblance to known elements of basal discoglossids (e.g., the Middle Jurassic *Eodiscoglossus oxoniensis*, Evans et al., 1990) are tentatively associated with the first iliac type. Those elements showing a different morphology are described with the second frog. It must be stressed, however, that these attributions are provisional and speculative; they have not been used in taxon diagnoses. In some instances, for example the Type 2 premaxillae and maxillae, there is direct evidence of association in the form of overlap surfaces. In many other cases, as outlined in the discussion section that follows, it is the combination of features from different attributed elements that strengthens the argument.

Institutional abbreviations appear as follows: AMNH, American Museum of Natural History; MCM, Muséum national d'Histoire naturelle, Paris, France.

SYSTEMATIC PALEONTOLOGY

Anura Rafinesque, 1815

Discoglossidae Gunther, 1859

aff. Enneabatrachus sp. Evans and Milner, 1993

(Fig. 2A–G)

Attribution.—The general iliac morphology of the Type 1 Anoual frog matches that of discoglossid frogs as characterized by Estes and Sanchíz (1982a) and Sanchíz (1998)

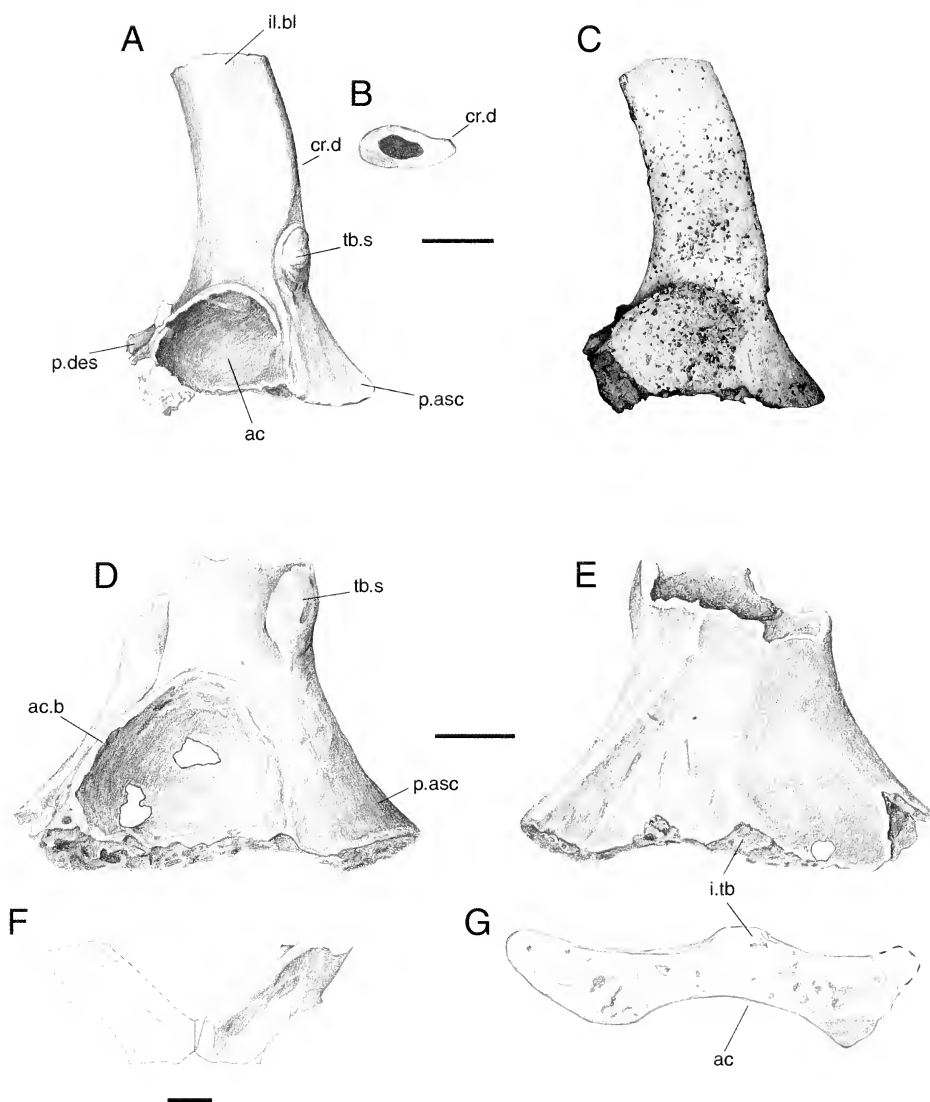


Fig. 2.—aff. *Enneabatrachus*, ilium. A–C, MCM 60, holotype left ilium in A. Lateral, B. Shaft cross-section, C. Scanning electron micrograph, lateral view. D–G, MCM 59, Paratype left ilium, in D. Lateral view, E. Medial view, F. Ventral view to show approximate angle of articulation based on alignment of the interiliac tubercle, and G. Cross-sectional views. Scale bars = 1 mm. White areas are matrix.

(large ovoid dorsal tubercle, well-developed processus ascendens), and broadly resembles that of several known taxa recovered from Jurassic and Early Cretaceous localities (e.g., *Enneabatrachus*, Evans and Milner, 1993; *Eodiscoglossus oxoniensis*, Evans et al., 1990; *Paradiscoglossus*, Estes and Sanchíz, 1982b; unnamed Japanese form, Evans and Manabe, 1998). It differs from the living *Bombina* and *Barbourula*, and the Cretaceous *Scotio-phryne* (Estes, 1977), in having a prominent tuber superior; from *Discoglossus*, *Paradiscoglossus*, *Wealdenbatrachus* (Fey, 1988) and described species of *Eodiscoglossus*

(Hecht, 1970; Vergnaud-Grazzini and Wenz, 1975; Evans et al., 1990) in the absence of a pronounced dorsal crest and of a supraacetabular fossa; and from *Enneabatrachus hechti* and *Eodiscoglossus* in the presence of an interiliac tuber, however weak. However, in terms of general blade shape, position and size of the tuber superior, absence of a supracetabular fossa, the shape of the acetabulum (smoothly rounded) and some extension of the ventral acetabular rim, the closest similarity is between the Anoual form and the Late Jurassic Morrison *Enneabatrachus hechti* (Evans and Milner, 1993). The main differences are the apparent absence of an interiliac tuberosity in *Enneabatrachus hechti*, a greater degree of ventral expansion of the acetabular rim, and a greater dorsal extension of the tuber superior beyond the margin of the bone, such that there is a distinct dorsal prominence in medial view, a feature not seen in the Anoual form. Very little work has been done on intra- and interspecific variation in frogs, but considerable interspecific differences can occur in the size and shape of the tuber superior and dorsal prominence (see figures in Sanchíz, 1998; MJ/SE personal observation), and there are differences in blade shape between *Eodiscoglossus oxoniensis* and *E. santonjae* (SE personal observation).

Description

Ilium.—The Type 1 ilium is represented by 13 specimens, the most informative of which are MCM 59 and MCM 60 (Fig. 2A–G). The acetabulum is shallow with a relatively unexpanded acetabular rim (Fig. 2A, C, D), although the ventral margin is deeper than the dorsal one. There is a short, flared pars ascendens that expands medially to form a buttress-like ridge, but the pars descendens is not significantly developed. Medially, there is a weak centrally placed interiliac tuberosity (Fig. 2E, G), and the two ilia would meet at an angle estimated as roughly 90° (Fig. 2F). The acetabular region grades smoothly into the iliac blade, with the latter never less than one-half the basal width. The iliac blade is ovoid in cross-section (Fig. 2B). There is a small dorsal crest, but this is poorly demarcated from the rest of the blade. The crest is certainly less developed than that of the Type 2 ilium, even though all specimens of the latter are of smaller overall size. The tuber superior is prominent (Fig. 2A, D), but does not extend beyond the dorsal margin of the bone. Its long axis is directed anteriorly.

Premaxilla.—The premaxillae are paired dermal bones that form the most anterior part of the maxillary arch (Trueb, 1973). Anoual premaxillae all have 16–21 tooth positions and a short, moderately wide, parallel-sided alary process (roughly a third of the total labial width) containing a recess for the anterior end of the nasal cartilage (Figs. 3B, E). Both types have bicuspid, pedicellate teeth (Fig. 3G–H), but they differ in the form of the alary process and that of the pars palatina.

Type-1 premaxillae (e.g., MCM 62, Fig. 3A–C) have an alary process that is more sharply angled (45°) posteriorly. There is a small but prominent tubercle at the labio-medial base. This is present on even the smallest Type 1 specimens (e.g., MCM 63) and thus seems to be characteristic of this premaxillary type. The pars palatina is narrowest at its mid-point while medially it extends back into a lanceolate projection. The exaggerated medial curve of this projection results in the formation of a notch (n, Fig. 3A) where the pars palatina meets the vertical pars dentalis. The lateral margin of the pars palatina also expands but to a smaller degree, and is marked by a series of ridges, grooves, and tubercles that give it a roughened, convoluted appearance. This premaxillary type lacks any overlap surface for the maxilla, and the two bones presumably abutted.

Maxilla.—Numerous maxillary fragments occur amongst the Anoual material and most conform to a single type (Type 1). A second kind (Type 2, see below) is known only from

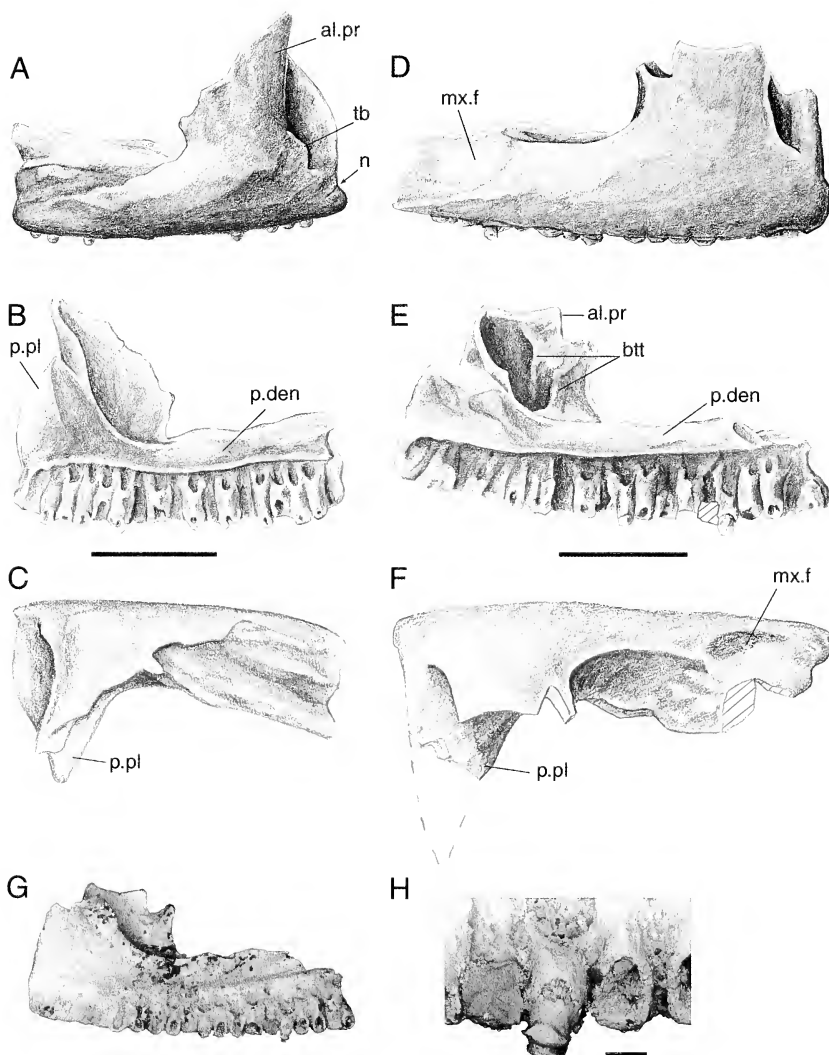


Fig. 3.—Anoual anuran premaxillae. A–C, MCM 62, Type 1 right premaxilla in A. Labial, B. Lingual, and C. Dorsal views. D–F, MCM 61, Type 2 right premaxilla in D. Labial, E. Lingual, and F. Dorsal views. G–H, Scanning electron micrographs of MCM 61, with G. Lingual view, H. Enlargement to show pedicellate bicuspid tooth. Scale bars = 1 mm except G (0.5mm) and H (0.1mm). Hatched areas are regions of broken bone.

anterior and posterior fragments and differs primarily in having larger anterior teeth and a groove on the labial surface. Neither type bears dermal ornament.

Type 1 (Fig. 4A–F) is represented by sufficient specimens (e.g., MCM 64, 65, 66) to permit an estimate of around 50–55 tooth positions. The teeth have relatively short circular or ovoid pedicels, the height being no more than two or three times the width. The maxillary rostrum is incompletely known, but the anterior part (MCM 66, Fig. 4D) is labially expanded and lingually concave. Its relationship to the premaxilla is unclear, but, at least as preserved, it lacks an edentulous overlap process, unlike Type 2. Above the tooth row, the crista dentalis is robust and cylindrical in cross-section (MCM 65, Fig. 4B–D),

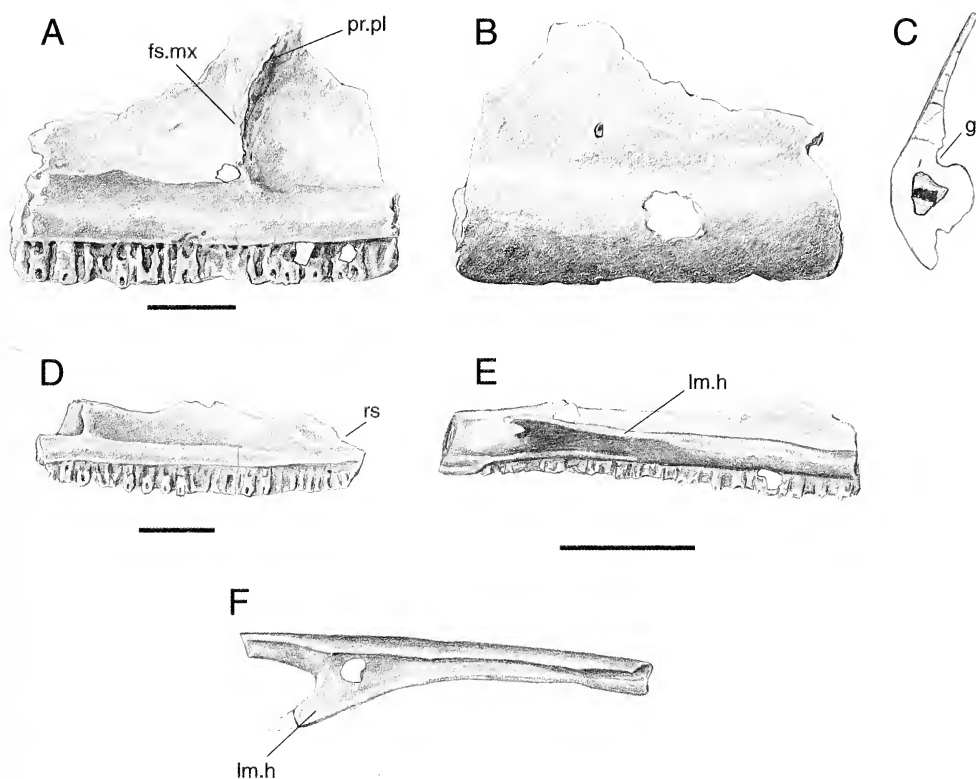


Fig. 4.—Anoual Type 1 anuran maxillae. A–C, MCM 65, central region of a left bone, in A. Medial, B. Lateral, and C. Cross-sectional views. D. MCM 66, anterior region of left bone, medial view. E–F, MCM 64, posterior region of left bone, in E. Medial, and F. Dorsal views. Scale bars = 1 mm. White areas are matrix.

becoming more horizontal posteriorly (as the lamina horizontalis). It terminates postero-dorsally by expanding into a barb or fluke-like process (e.g., MCM 64, Fig. 4E, F). The processus palatinus is weakly developed and delimits a posterior cavity, the fossa maxillaris (fs.mx, Fig. 4A). From this cavity a gutter (g, Fig. 4C) runs backward along the dorsal surface of the crista dentalis, expanding posteriorly as the lamina does (Fig. 4E–F). The labial surface of all specimens is smooth and convex.

Atlas.—The atlas (cervical of Trueb, 1973) is easily distinguished from other vertebrae by the paired anterior cotyles for articulation with the occipital condyles of the skull. Four atlantal centra, representing two distinct morphologies, have been recovered at Anoual. In both cases, however, the atlantes match the ‘type II’ morphology of Lynch (1971)—the cotyles fully separated, but only by a relatively small gap.

The Type 1 Anoual atlas (MCM 79, 80) is trapezoidal and relatively long (Fig. 5A–E, J). The anterior cotyles are deep and oval, with their long axes inclined dorsolaterally at roughly 10° (Fig. 5A, B). They are fully separated by a slight anterior projection. Posteriorly there is a rounded imperforate cotyle suggesting opisthocoely. The centrum itself is dorsoventrally flattened, with a smooth or pitted ventral surface that might be indicative of immaturity. The neural arches are broken away but the pedicels appear to narrow sharply from a broad base.

Sacral vertebra.—Like the atlas, the sacrum is also unmistakable (Fig. 6A–H). Type 1 is represented by four specimens, from both juvenile and fully adult individuals. MCM 83

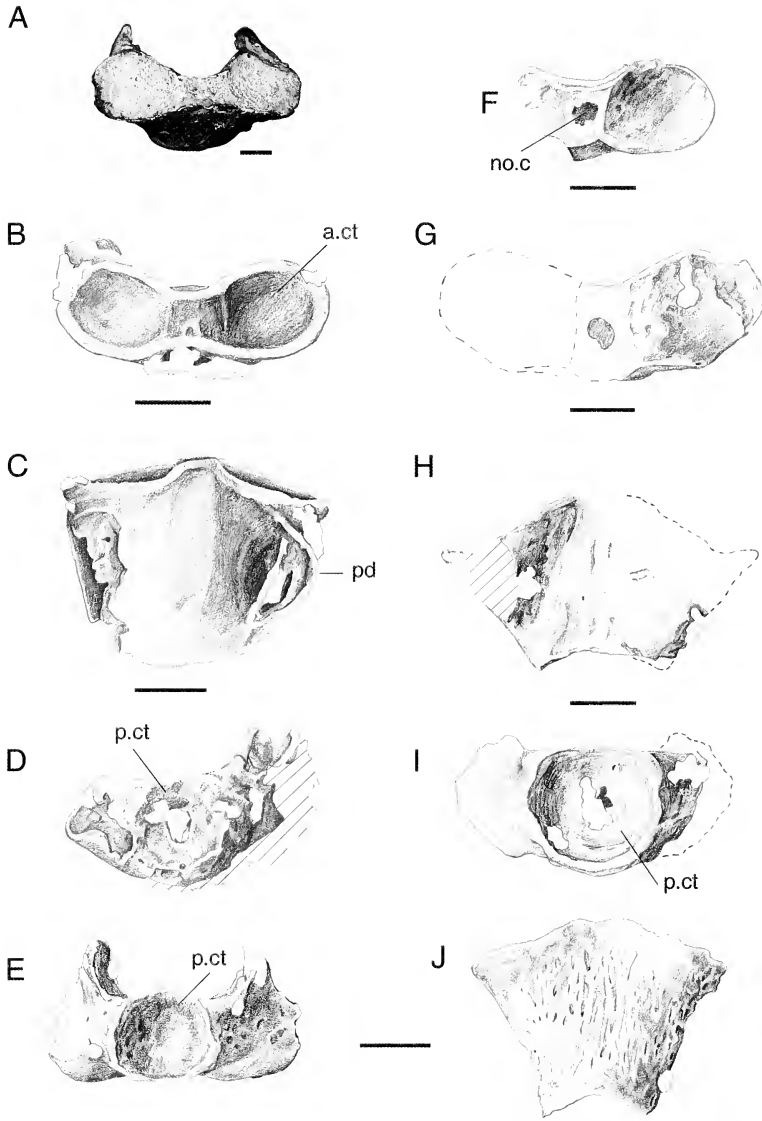


Fig. 5.—Anoual anuran atlantes. A–E, J, Type 1 atlantes, with A. MCM 79, scanning electron micrograph, anteroventral view. B–D, MCM 80, in B. Anterior, C. Dorsal, and D. Posterior views. E, J, MCM 79, in E. Posterior and J. Ventral views. F–I, Type 2 atlantes, F. MCM 82, anterior view. G–I, MCM 81, in G. Anterior, H. Dorsal, and I. Posterior views. Scale bars = 1 mm except A (0.5 mm). White areas are matrix; hatching denotes broken surfaces.

(Fig. 6A–D), an adult sacral, is by far the most complete. It is short, wide, and robust with fully formed joint surfaces, a depressed oval anterior condyle and paired posterior condyles separated by a very small remnant of the notochordal canal (Fig. 6A, B). The last presacral vertebra was thus clearly opisthocelous or diplasiocelous (bicotylar). The neural arch is complete, with a thick weakly crested dorsal lamina and robust pedicels supporting strong, posteriorly directed, cylindrical transverse processes and large expanded

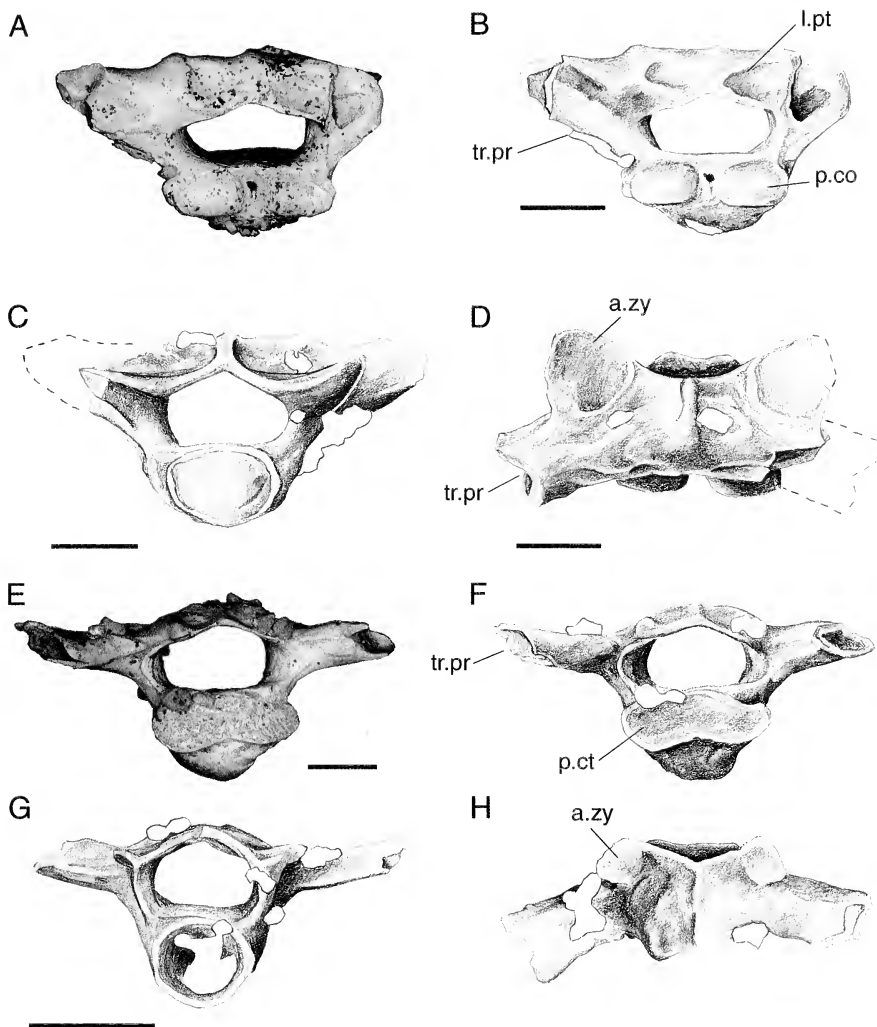


Fig. 6.—Anoual anuran sacra. A–D, MCM 83, Type 1 sacral in A. Scanning electron micrograph, posterior view, B. Posterior view, C. Anterior view, D. dorsal view. E–H, MCM 85, Type 2 sacral, in E. Scanning electron micrograph, posterior view, F. Posterior view, G. Anterior view, H. Dorsal view. Scale bars = 1 mm. White areas are matrix.

anterior zygapophyses. The posterior margin of the arch is straight with paired pits for spinal ligaments. MCM 84 (not figured) is a left vertebral fragment interpreted as a juvenile Type 1. It is notochordal but the posterior surface is clearly divided into discrete articular condyles. There is also no anterior condyle, but the notochordal cotyle bears a raised lateral edge that presumably represents a stage in the development of the adult condyle. Several of the immature presacral centra show a similar condition and can be attributed to this vertebral type (see below).

Post-atlantal presacral vertebrae.—The atlantes and sacra together suggest that of the two Anoual frogs, one is opisthocoelous and the other is amphicoelous or procoelous (see below). However, although two morphotypes are present amongst the remaining vertebrae,

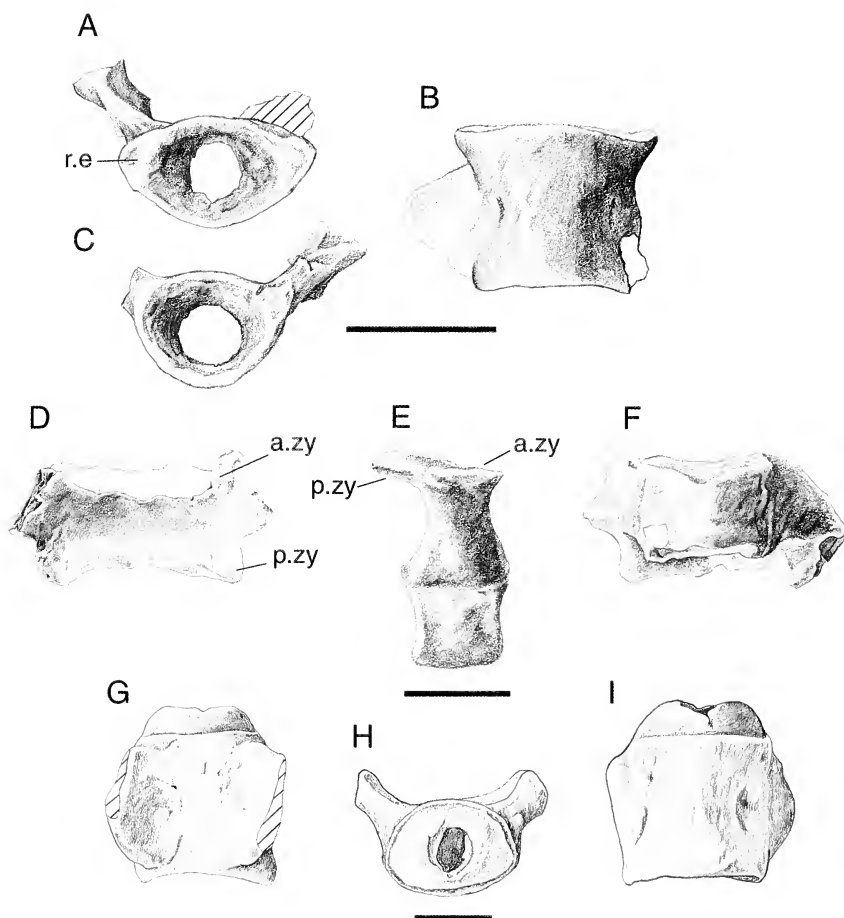


Fig. 7.—Anoual anuran presacrals, Type 1. A–C, MCM 87, Type 1 centrum in A. Anterior, B. Ventral, and C. Posterior views. D–F, abraded Type 1 vertebra, MCM 206, in D. Dorsal, E. Lateral, and F. Ventral views. G–I, MCM 207, in G. Dorsal, H. Anterior, and I. Ventral views. Scale bars = 1 mm. White areas are matrix; hatching denotes broken surfaces.

most of the centra are amphicoelous (Fig. 7A–F, Fig. 11A–B). Either these amphicoelous presacral vertebrae represent additional taxa, or they are immature.

Type 1 amphicoelous vertebrae have centra that are usually wider than long, with short, flat, neural arch laminae (Fig. 7D, E). The relative positions of the zygapophyses and arch margins suggest a degree of imbrication. The transverse processes are rounded in cross-section but usually broken at the base. MCM 78 (not figured) is an exception in preserving more distal parts of the transverse process. A suture line separates the proximal portion of the process from the tip, suggesting that a free rib has become fused. In general morphology, these vertebrae resemble the bicondylar Type 1 sacral, except that they are notochordal and amphicoelous, rather than opisthocelous. However, they are also closer in size to the juvenile Type 1 sacrum. As noted above, this vertebra (MCM 84) lacks an anterior condyle but has an articular surface with a raised lateral edge. This condition is found in at least some of the Type 1 presacrals (e.g., MCM 87, Fig. 7A, r.e), suggesting

they may also belong to an animal that was opisthocoelous when fully adult. This conclusion is supported by MCM 207, a more mature vertebral centrum bearing an incomplete anterior condyle (Fig. 7G–I). Isolated Type 1 centra closely resemble those previously described for Jurassic and Early Cretaceous discoglossids (e.g., *Eodiscoglossus*, Estes and Sanchíz, 1982a; Evans et al., 1990).

Scapula.—The anuran pectoral girdle is adapted to absorb the stress of saltorial locomotion (Trueb, 1973). The scapula is generally short and broad with separate articular surfaces for the clavicle (pars acromialis) and coracoid (processus glenoidalis) divided by a scapular cleft (lost in some taxa, e.g., *Ascaphus*, *Pipa*).

Type 1 scapulae (e.g., MCM 93, Fig. 8A, D, MCM 94, Fig. 8G) have a short broad scapular blade that is mediolaterally flattened. No trace of the anterior margin is preserved. The bone is weakly cleft proximally, with the interglenoid sinus directed mediolaterally. The pars acromialis is thick (mediolaterally) and forms a distinct anterior wall to the scapula cleft. The pars glenoidalis is prominent and faces posteriorly.

Anura Rafinesque, 1815
Mesobatrachia Laurent, 1979
Genus *Aygroua*, **new genus**

Etymology.—From Ay-grou, a Moroccan Berber word for frog.

Aygroua anoualensis, **new species**
(Fig. 9A–D)

Etymology.—From the area of the type locality, Anoual.

Holotype.—The proximal part of a right ilium, Muséum national d'Histoire naturelle, Paris, MCM 183.

Type locality and horizon.—2.5 km East South East of Ksar Met-Lili, Anoual syncline, 100 km east of the city of Anoual, Talsint Province, Morocco (International coordinates: 3°13'50"W; 32°42'9.5"N); Morocco B sequence of the 'couches rouges', Lower Cretaceous, Berriasian.

Referred material.—Ilium MCM 57 and eight further iliac specimens. A number of other skeletal elements are more tentatively assigned to this taxon but do not feature in the diagnosis. These include the following: a premaxilla, MCM 61; maxillae, MCM 67–69; atlantes, MCM 81, 82; a sacral vertebra, MCM 85; presacral vertebrae, MCM 77, 86, MCM 208–210; and scapulae, MCM 95–96.

Diagnosis.—Small anuran having an iliac blade with a strong dorsal crest; strong dorsal prominence but no tuber superior; flared ventral acetabular rim which is visible in medial view and obscures pars descendens laterally; and large, ventrally placed interiliac tuberosity supported by a strong medial buttress.

Remarks.—*Aygroua* differs from most discoglossids in having an ilium showing the following combination of features: a strong dorsal prominence but lacking the typical ovoid tuber superior; preacetabular narrowing of the iliac blade, and a strong medial iliac synchondrosis (Fig. 9C). *Aygroua* resembles the living discoglossid *Bombina* in the preacetabular narrowing and medial synchondrosis, but differs in the expansion of the dorsal crest and prominence. *Aygroua* differs from *Notobatrachus* (Middle Jurassic, Argentina, Báez and Basso, 1996), *Mesophryne* and *Callobatrachus* (Early Cretaceous, China, Gao and Wang, 2001), and the living *Leiopelma* and *Ascaphus*, in having a strong dorsal crest; differs from pelobatoids in lacking the spiral groove on the dorsal margin of the iliac shaft; and differs from known rhinophrynids (including the basal *Rhadinosteus*, Henrici, 1998b), but resembles pipimorphs, in having a strong interiliac tuberosity. Comparison with the Early Cretaceous pipoids *Thoraciliacus* and *Cordicephalus* (Nevo,

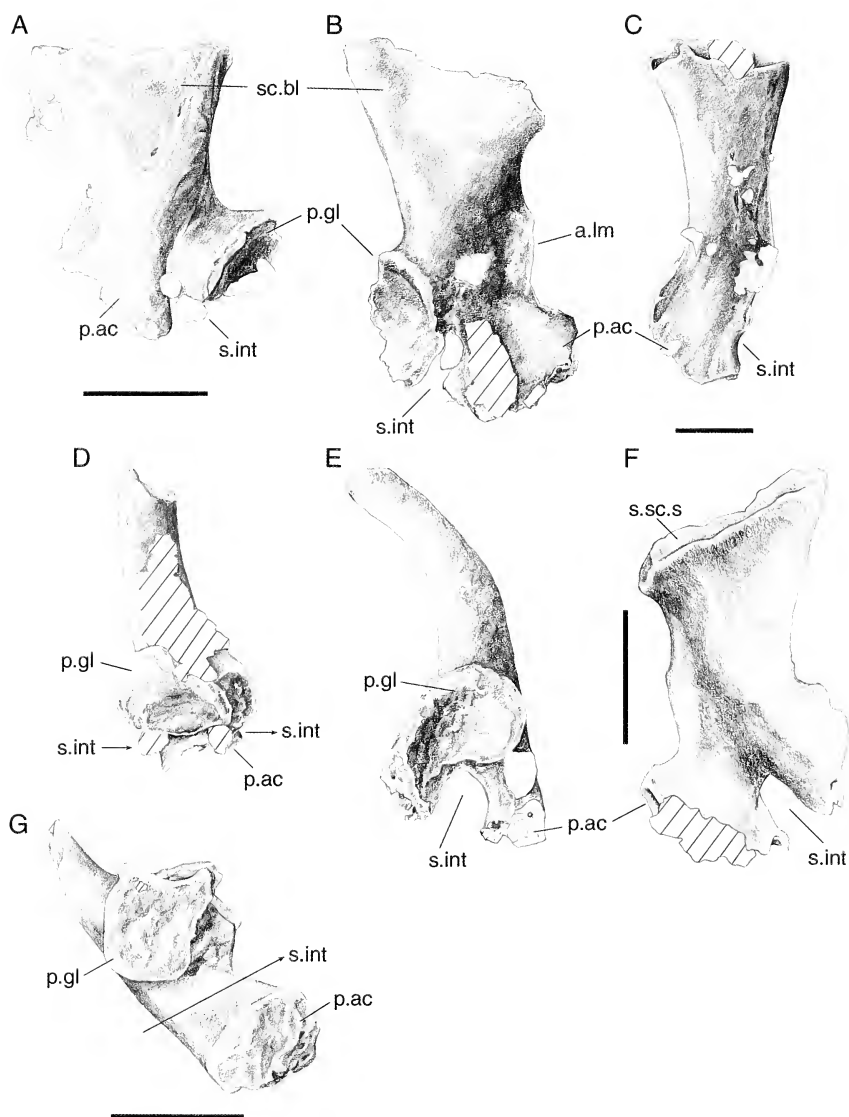


Fig. 8.—Anoual anuran scapulae. A–C, lateral views, with A. MCM 93, Type 1, B. MCM 95, Type 2. C. MCM 96, ?aberrant Type 2. D–E, posterior views of D. MCM 93, and E. MCM 95. F. MCM 95, medial view. G. MCM 94, Type 1 scapula, posterior view to show lateromedial course of scapular cleft. All scale bars = 1 mm, A, B, D and E to the same scale. White areas are matrix; hatching denotes broken surfaces.

1968; Trueb, 1999) is made difficult by the difference in preservation (3-D disarticulated vs. 2-D articulated), and by the lack of detailed information on iliac shape (Trueb, 1999). There are, however, striking differences in, for example, premaxillary, sacral, and urostylar morphology between *Thoraciliacus* and *Cordicephalus* on the one hand (triangular alary process of premaxilla; flared sacral transverse processes; fused postsacrals) and the anuran elements preserved at Anoual (parallel-sided alary processes; unflared or slightly flared sacral transverse processes; no postsacrals).

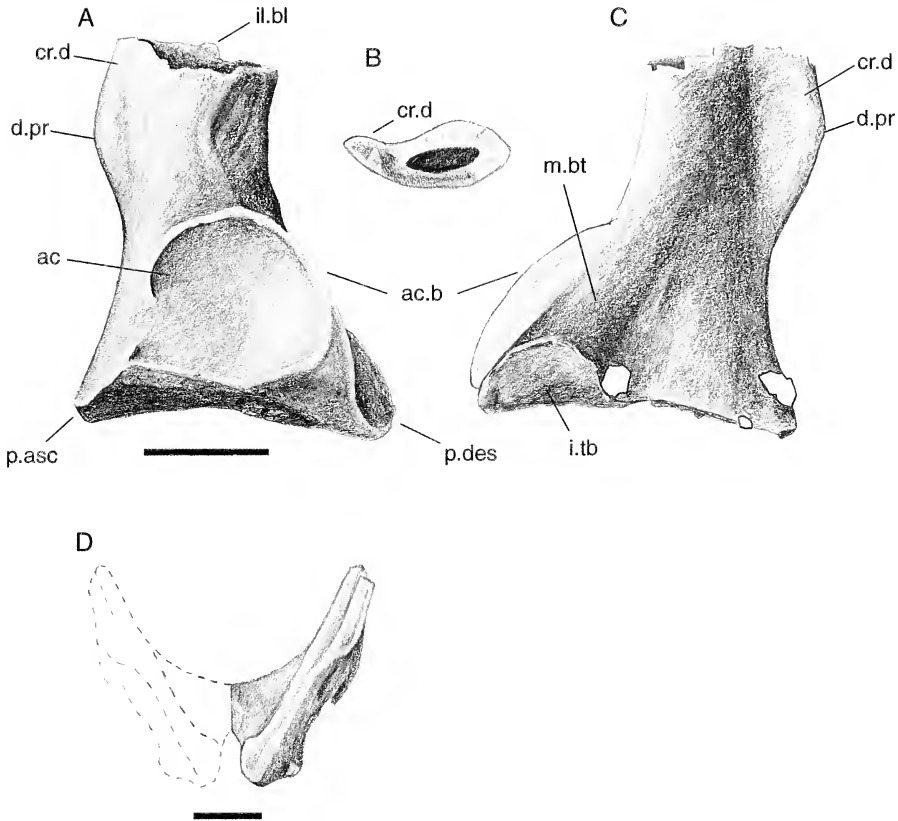


Fig. 9.—*Aygroua anoualensis*, gen. et sp. nov., holotype right ilium, MCM 183, in A. Lateral, B. Cross-section of shaft, C. Medial views, D. Posterior view to show approximate angle of articulation based on alignment of the interiliac tubercle. Scale bars = 1 mm. White areas are matrix.

Description

Ilium.—The *Aygroua* ilium is represented by nine specimens, the most informative of which are MCM 183 (Fig. 9) and 57. These ilia have a deep asymmetrical acetabulum. The ventral acetabular rim is greatly expanded to the extent that it is visible in medial view and almost completely obscures the pars descendens (Fig. 9A). The pars ascendens is prominent but shows little expansion. The pars descendens is larger and separated from the acetabular rim by a distinct groove. Medially (Fig. 9C), the acetabulum is strengthened by a large posterior buttress leading to the iliac tuberosity, a feature that may be associated with an aquatic lifestyle (Vergnaud-Grazzini and Hoffstetter, 1972). A second, deeper groove separates this buttress from the pars descendens. The buttress significantly increases the size and surface area of the interiliac synchondrosis. The interiliac angle can be estimated at 60° (Fig. 9D).

The iliac blade is relatively slender, but it bears a prominent crest (Fig. 9B, D) that in some specimens accounts for up to half the width of the blade at its most dorsal point. Overall, there is a sharp distinction between the basal, acetabular region of the ilium and the blade, the latter being only about one-third of the proximal width. There is a shallow but elongated dorsal prominence (d.pr) with a thickened margin but no development of

a tuber superior as such (Fig. 9A). The prominence gives the dorsal margin a strong sigmoidal outline.

Premaxilla.—The Type 2 premaxilla (e.g., MCM 61, Fig. 3D–H) resembles those of Type 1 in tooth number and general form, and has a smooth, convex labial surface. The alary process has both medial and lateral buttresses. Together these create four sharp edges: medial, posteromedial, lateral, and posterolateral. Between the two medial edges there is a very deep cavity, while the two lateral edges frame a smooth, concave surface that sometimes displays one or two small basal foramina. Lingually, the pars palatina extends back almost horizontally and has a smooth margin. The distal end of the extension is unknown, but the proximal base is less symmetrical than that of Type 1. This premaxillary type has a basin-like lateral overlap surface for the maxilla (mx.f, Fig. 3F).

Maxilla.—The Type 2 maxilla is much rarer than Type 1, and is represented only by four anterior fragments (e.g., MCM 67, 68, Fig. 10A–D) and one posterior fragment (MCM 69, Fig. 10E–F). The anterior and posterior fragments are tentatively associated by the presence of a labial groove, although the tooth morphology differs. Anteriorly (Fig. 10A, C), the tooth pedicels are narrow in cross-section, and are relatively taller than those of Type 1. Posteriorly (Fig. 10E), they are shorter and smaller. A similar disparity in tooth size does, however, occur in other known taxa (e.g., *Eodiscoglossus oxoniensis*, Evans et al., 1990). The Type 2 rostrum is lingually convex rather than concave and the labial surface differs from that of Type 1 in having a wide but shallow groove (l.gr, Fig. 10F) on the otherwise flat labial surface (Fig. 10B, D, F). In cross-section, this groove has the effect of shifting the crista dentalis labially, giving the bone the appearance of having a labially expanded margin or skirt. The rostral area also differs in another, potentially more significant, way from Type 1. It has an edentulous anterior premaxillary process (ed. rs, Fig. 10A, B) that matches the facet on the Type 2 premaxilla, suggesting an overlap between the maxilla and premaxilla. Anteriorly, the lamina horizontalis bears a ventral gutter that slopes upward. The processus palatinus is not preserved, but one specimen (MCM 68, Fig. 10C–D) shows the lamina horizontalis beginning to expand dorsally; this may represent the anterior limit of the processus palatinus. In the posterior region, the labial groove slopes gently, corresponding to the area on the lingual surface between the crista dentalis and the lamina horizontalis. The latter is shelf-like in cross-section, projecting twice as far as its width (Fig. 10E). No pronounced gutter is present ventrally or dorsally. The lamina is not parallel to the crista dentalis but slopes gently upward to a high abrupt posterior termination. The result is a large gap between it and the tops of the small cylindrical tooth pedicels.

Atlas.—Type 2 atlantes (MCM 81, 82) are broadly similar to those of Type 1 but are relatively shorter and wider, with an overall pentagonal shape (Fig. 5H). The anterior cotyles are separated by a small intervening surface that is perforated in both specimens by the remains of the notochordal canal, suggesting immaturity (Fig. 5F–G). The posterior face of the centrum contains a rounded cotyle that is perforated by a small notochordal canal (Fig. 5I).

Sacral vertebra.—MCM 85 (Fig. 6E–H) is a sacral vertebra of rather different morphology from those of Type 1. It is much more gracile than the adult Type 1 (even allowing for the smaller size), and the body of the bone is proportionally longer. Although of similar size to the juvenile Type 1, the posterior articular surface (Fig. 6E–F) is undivided and linear. It is slightly recessed and clearly held a cartilaginous (fibrocartilaginous) pad so that the sacrococcygeal joint was either a synchondrosis, the primitive condition (Trueb, 1973) seen in leiopelmatids, or an immature stage in the development of either monocondyly or sacro-urostylar fusion. Anteriorly, the centrum bears a large rounded cotyle, suggesting the last presacral vertebra was either procoelous or amphicoelous. The transverse processes angle posteriorly as in Type 1, but they differ in being dorsoventrally

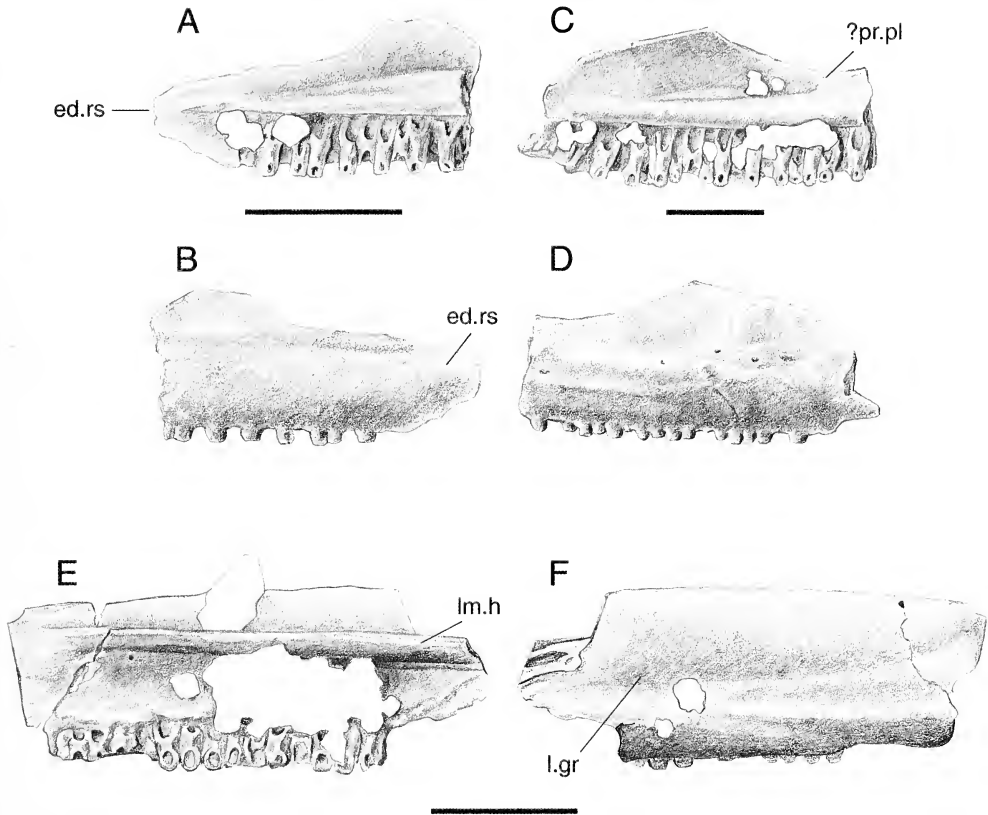


Fig. 10.—Anoual Type 2 anuran maxillae. A–B, MCM 67, anterior region of right bone, in A. Medial, and B. Lateral views. C–D, MCM 68, anterior region of right bone in C. Medial, and D. Lateral views. E–F, MCM 69, posterior region of right bone, in E. Medial, and F. Lateral views. Scale bars = 1 mm. White areas are matrix.

compressed with a slight distal flaring that suggests a gradual expansion towards the tips. The neural arch is more vaulted than that of Type 1, with a low median crest, relatively much smaller anterior zygapophyses, and no posterior pits for spinal connective tissues.

Post-atlantal presacral vertebrae.—Type 2 presacrals (e.g., MCM 77, 86, MCM 208–210) are characterized by several features: the centra are proportionally longer than those of Type 1; the neural arch pedicels are broad-based; the dorsal lamina is arched, anteriorly inclined, and has a moderately developed neural spine; and there is evidence of imbrication. The transverse processes are placed high on the neural arch and are more dorsoventrally compressed than those of Type 1 vertebrae. The majority of Type 2 vertebrae are amphicoelous and notochordal (e.g., MCM 77, Fig. 11A, B), with well-rounded anterior and posterior cotyles. However, the largest specimen (MCM 86, Fig. 11C–E), presumably an adult, is procoelous, with a fully developed posterior condyle. Nonetheless, the rounded cotyle and the central pit in the condyle suggest that this procoelously developed via a perichordal stage. As such, it does not fit Trueb's (1973) definition of procoely (derived from holochordy) but would fall within her category of anomocoelous, where centra are biconcave with a free intervertebral disc that adheres to the posterior end of the centrum without actually fusing to it, or fuses only at the adult stage. This is said to be a feature of terrestrial taxa (Trueb, 1973).

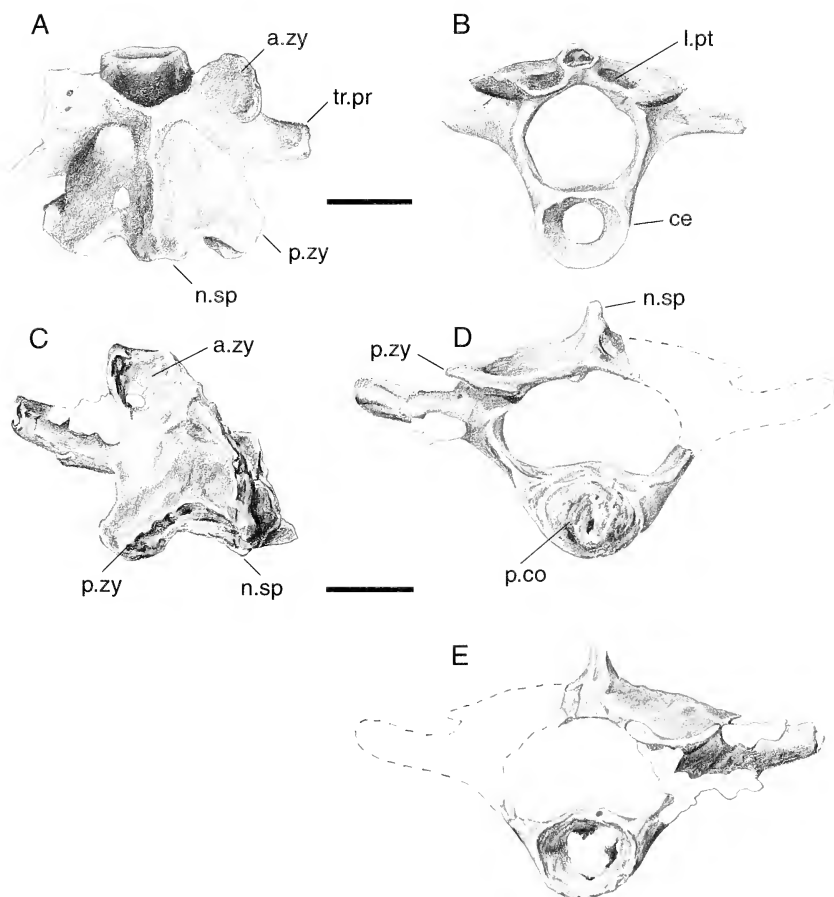


Fig. 11.—Anoual anuran presacral, Type 2. A–B, MCM 77, immature Type 2 presacral, in A. Dorsal, and B. Posterior views. C–E, MCM 86, mature Type 2 presacral, in C. Dorsal, D. Posterior, and E. Anterior views. Scale bars = 1 mm. White areas are matrix.

Scapula.—Type 2 scapulae (e.g., MCM 95, Fig. 8B, E, F) have a longer, narrower blade than that of Type 1. This flares distally into the suprascapular attachment and has a distinct crest (anterior lamina) along the anterior margin. The edges are complete in MCM 95, and the blade was clearly narrower than that of Type 1. Proximally the bone is strongly bifurcate with a narrower cleft that is long and directed posterolaterally-anteromedially. The pars acromialis is mediolaterally thin, while the pars glenoidalis is ventrally extended and flared. The glenoid faces posterolaterally. MCM 96 (Fig. 8C) resembles the Type 2 scapulae in all respects, except for the much taller blade. Either it represents a third frog taxon in the assemblage or it is a variant (possibly pathological) of the Type 2 scapula. A tall blade like this is found in the living pelobatid *Scaphiopus* (Sánchez, 1998).

ADDITIONAL ANURAN SKELETAL ELEMENTS

Introduction.—A subset of skeletal elements shows no characters that would permit even tentative attribution to one or other frog taxon. These include the mandibles, urostyles, and

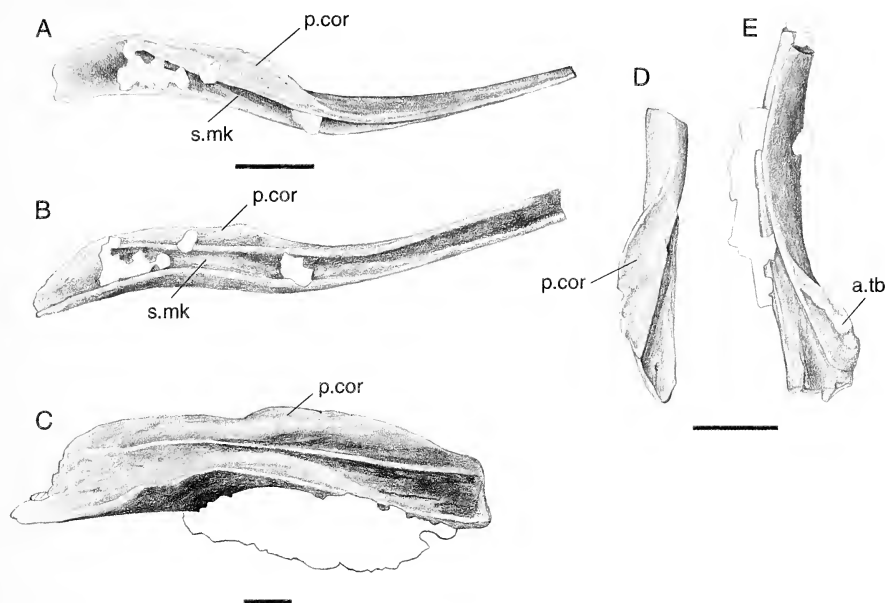


Fig. 12.—Anoual anuran angulosplenial. A–B, MCM 70, Type A right bone, in A. Dorsal, and B. Lateral views. C. MCM 71, Type A, right bone, in lateral view. D–E, comparison of D. MCM 72 (Type A, right bone) with E. MCM 74 (Type B, left bone) in dorsal view. Scale bars = 1 mm. White areas are matrix.

elements of the fore- and hindlimbs. In this section, where two morphotypes can be distinguished, they are designed Type A and Type B to preclude confusion with Types 1 and 2 as used above.

Mandible.—The anuran mandible consists of two bones (with or without ossified mentomeckelians)—the anterior dentary and the posterior angulosplenial. At Anoual, two types of angulosplenial are distinguished primarily by the anterior morphology of the processus coronoideus. Four specimens are confidently attributed to Type A (e.g., MCM 70–72; Fig. 12A–D) on the basis of a well-defined processus coronoideus with sharp lingual and labial edges. MCM 71 (Fig. 12C) is the largest specimen, presumably from an older individual. The processus coronoideus is slightly convex with a posterior gutter and a thin, raised, lingual edge. The small specimens possess an almost flat processus coronoideus, with the lingual edge slightly raised posteriorly while the labial edge is more prominent anteriorly. The lingual projection of the processus coronoideus is shelf-like and extends horizontally and medially.

A further four specimens (e.g., MCM 74, 75, 76, Fig. 12E) can be attributed to a second angulosplenial type. All preserve a small anterior part of the processus coronoideus (MCM 74, Fig. 12E) that is shallower than that of Type A (e.g., MCM 72, Fig. 12D), with a sharp labial edge and a rounded lingual edge bearing a weak anterior tubercle (a. tb, Fig. 12E). In addition, the process extends lingually at an oblique dorso-medial angle and its abutment with the rest of the bone is more gradual than that of Type A.

Urostyle.—The urostyle (or coccyx in Trueb, 1973) is formed by the fusion of post-sacral tail vertebrae. Five urostyles have been recovered, and they fall into three morphotypes—Type A (MCM 88, 89), Type B (MCM 90, 91), and a final specimen (MCM 92) that may be an aberrant form of Type A.

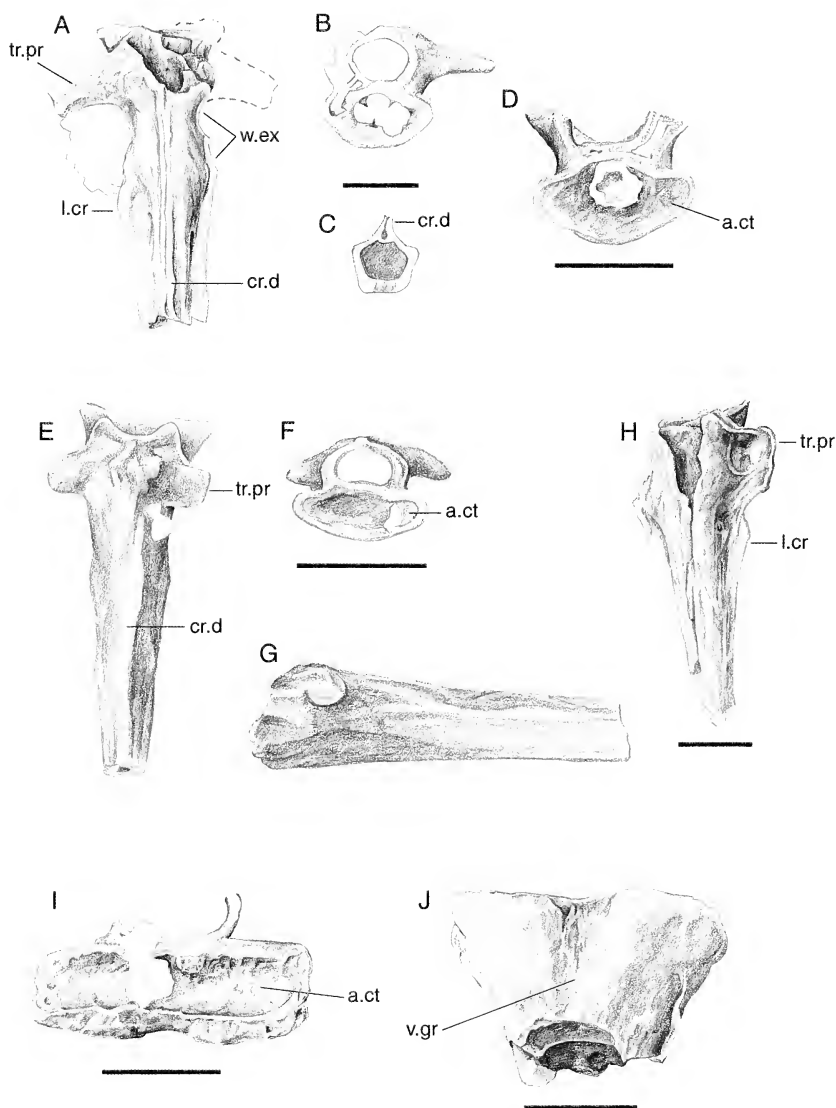


Fig. 13.—Anoual anuran urostyles. A–C, MCM 88, Type A urostyle, in A. Dorsal, B. Anterior, and C. Posterior cross-sectional views. D. MCM 89, Type A urostyle, anterior view. E–G, MCM 90, Type B urostyle, in E. Dorsal, F. Anterior, and G. Left lateral views. H. MCM 92, aberrant possible Type B urostyle, dorsal view. I, J, MCM 91, in I. Anterior, and J. Ventral views. Scale bars = 1 mm. White areas are matrix.

Type A urostyles are distinguished by a rounded, but laterally expanded anterior articular surface; prominent dorsal and lateral crests; a smooth ventral surface; and a pattern of waisting-expansion-constriction occurring posterior to the transverse processes (Fig. 13A–D). Only one specimen (MCM 88) preserves a transverse process and this shows a distinct posterior curvature. The upper surface is fairly flat while the ventral surface is rounded and anteriorly thickened, expanding medially to form a strong buttress. Both specimens (Fig. 13B, D) retain patent notochordal canals anteriorly and are therefore

probably immature. The dorsal crest is relatively well developed, but narrow, extending forward to at least the level of the transverse process.

Type B urostyles lack the distinctive features of Type A and have a relatively wider, more depressed anterior articular surface (Fig. 13F, I). Where preserved, the transverse processes are robust but short (Fig. 13E). There are no prominent lateral crests, while the dorsal crest begins weakly but becomes stronger and wider posteriorly. The most complete Type B urostyle is MCM 90 (Fig. 13E–G). Despite being very small, there is no trace of an anterior notochordal perforation. MCM 91 (Fig. 13J) is significantly larger and bears a subtle anteroventral groove.

MCM 92 (Fig. 13H) is damaged anteriorly, but the anterior surface does not appear conspicuously wide. The transverse process is thin, flat and broad-based. Posteriorly, it effectively grades into a prominent lateral crest, although a small notch separates the process from the crest on the right side. The degree of development of this crest appears to be asymmetrical on the two sides of the bone. In the presence of a dorsal crest, relatively narrow anterior articulation, longitudinal crest and waisting, MCM 92 resembles Type A urostyles, the main difference being the shape of the transverse process. Asymmetry in the form of the urostyle transverse process has been reported in recent taxa (e.g., discoglossids, ranids, Roček, 2000) and in the Jurassic *Notobatrachus* (Báez and Basso, 1996:143), but levels of inter- and intraspecific variation are not well studied in frogs.

Forelimb elements.—Most humeral specimens preserve only the distal end. MCM 97 is an exception (Fig. 14A–D) in retaining part of the proximal shaft. The crista ventralis is moderately developed while the crista paraventralis is present but more subtle (Fig. 14B). However, since the degree of development of these crests may be related to sexual dimorphism rather than phylogeny (Roček, 1994), this feature is probably not significant. The long axis of the bone is straight and the distal humeral condyle (eminencia capitata) lies centrally. The condyle is large relative to the overall distal width (roughly 72%), while the ulna epicondyle is small and the radial side unexpanded. Although the Anoual humeri show variation in features such as the position of the olecranon scar and the definition of the lateral border of the fossa cubitalis ventralis, these features can be size-related (e.g., Evans and Milner, 1993, MJ/SE personal observations).

The radioulna is represented by two specimens, of which MCM 98 is the better preserved (Fig. 14E). The olecranon process is well developed, suggesting a terrestrial frog with strong limbs.

Hindlimb elements.—MCM 99 appears to be the proximal head of an anuran femur (Fig. 15A). It is small but exhibits a pronounced crista femoris. Tibiofibulae are far more commonly represented and can be divided into two types based on cross-sectional shape and the development of the crista cruris (Fig. 15B–C). Type A tibiofibulae (e.g., MCM 100, Fig. 15B) seem to be relatively longer than Type B. They are generally rounded, with a circular cross-section centrally and a figure of eight cross-section proximally. The crista cruris is subtle and rounded. The tibia and fibula are parallel although centrally the fibula warps towards the tibia. Grooves marking the separation of the two bones are limited to the proximal and distal ends. Type B elements (e.g., MCM 73, Fig. 15C) differ in being squarer in cross-section with at least one well-defined corner. A pronounced crista cruris is present on the proximal part of the tibia. The tibia and fibula are parallel although the slightly smaller fibula narrows centrally. Allowing for the more fragmentary nature of Type B bones, the grooves separating the tibia and fibula appear more extensive than those of Type A.

MCM 76 is a partial tibiale-fibulare (not figured). The components are completely separated except at the distal tips, which are slightly expanded and fused.

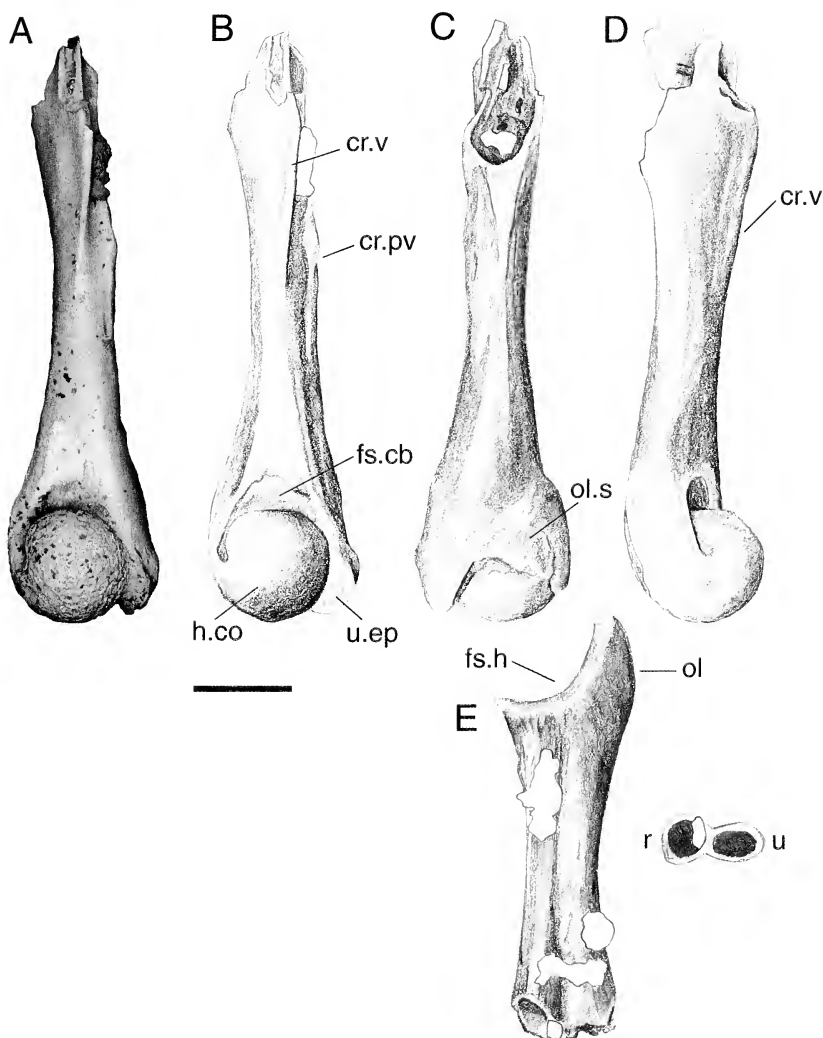


Fig. 14.—Anoual anuran forelimb elements. A–D, MCM 97, left humerus, in A. Scanning electron micrograph, ventral view, B. Ventral view, C. Dorsal view, D. Lateral view; E. MCM 98, radioulna. Scale bars = 1 mm. White areas are matrix.

DISCUSSION

Comparison

Introduction.—As far as we can determine, and allowing for two anomalous elements (the odd scapula, MCM 96, and urostyle, MCM 92), the Anoual remains are consistent with the presence of two distinct frog taxa in the deposit. Detailed cladistic analyses are obviously not possible with fragmentary material of this kind, but at least some of the skeletal elements preserved at Anoual are considered phylogenetically informative.

Ilium.—Ilia are the elements most commonly used in the diagnosis of anuran taxa from microvertebrate sites (Fig. 16). Widely used characters include the presence or absence of a dorsal crest; the shape of the blade and its relationship with the acetabular region; the

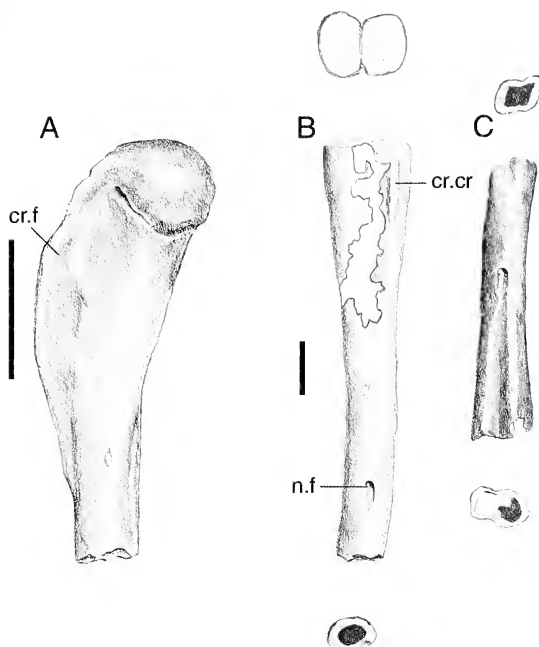


Fig. 15.—Anoual anuran hind limb elements. A. MCM 99, femoral head, lateral view. B. MCM 100, Type A tibiofibula, in dorsal view with proximal end and distal cross-section. C. MCM 73, Type B tibiofibula, dorsal view, with proximal and distal cross-sections. Scale bars = 1 mm. White areas are matrix.

presence, size and position of a tuber superior and/or dorsal prominence; the relative sizes of the partes ascendens and descendens; the degree of expansion, if any, of the acetabular rim; the presence or absence of a supraacetabular fossa; and the presence or absence, size, and position of any interiliac tuberosity (e.g., Sanchíz, 1998). On this basis, the Anoual ilia fall into two distinct morphotypes. Of these, one shows a close resemblance to the ilia of known Mesozoic discoglossids (particularly *Eodiscoglossus*, *Enneabatrachus*, *Paradisoglossus*, Fig. 16A–E) in the shape, size and position of the tuber superior, the shape of the iliac blade and its continuity with the acetabular region (no marked waisting), and a well-developed pars ascendens (Roček, 1994). As discussed above (Systematic Paleontology), the greatest similarity is with the Late Jurassic *Enneabatrachus hechti* from the Morrison Formation of the USA (Fig. 16A–B), although the Anoual forms differ in the presence of a weak interiliac tubercle, a less prominent tuber superior, and a less expanded ventral acetabular rim.

The second frog, *Aygroua*, has an ilium that is distinctive but not obviously attributable to a particular anuran clade. It differs from the ilium of most discoglossids in the shape of the blade, the presence of a dorsal prominence rather than a clear ovoid tuber superior, the relatively undeveloped pars ascendens, and the presence of a strong interiliac tuberosity. A strong, buttressed, interiliac tuberosity of this kind is found in pipimorph frogs (palaeobatrachids, pipids, e.g., Fig. 16F–H), and the flaring of the acetabular rim and the development of a dorsal prominence would be consistent with at least some of these groups (e.g., palaeobatrachids), as would the narrowing of the shaft immediately distal to the acetabulum (crests excepted) and the relatively low interiliac angle (Sanchíz and Roček, 1996; Trueb, 1996). The *Aygroua* ilium differs from that of living and fossil

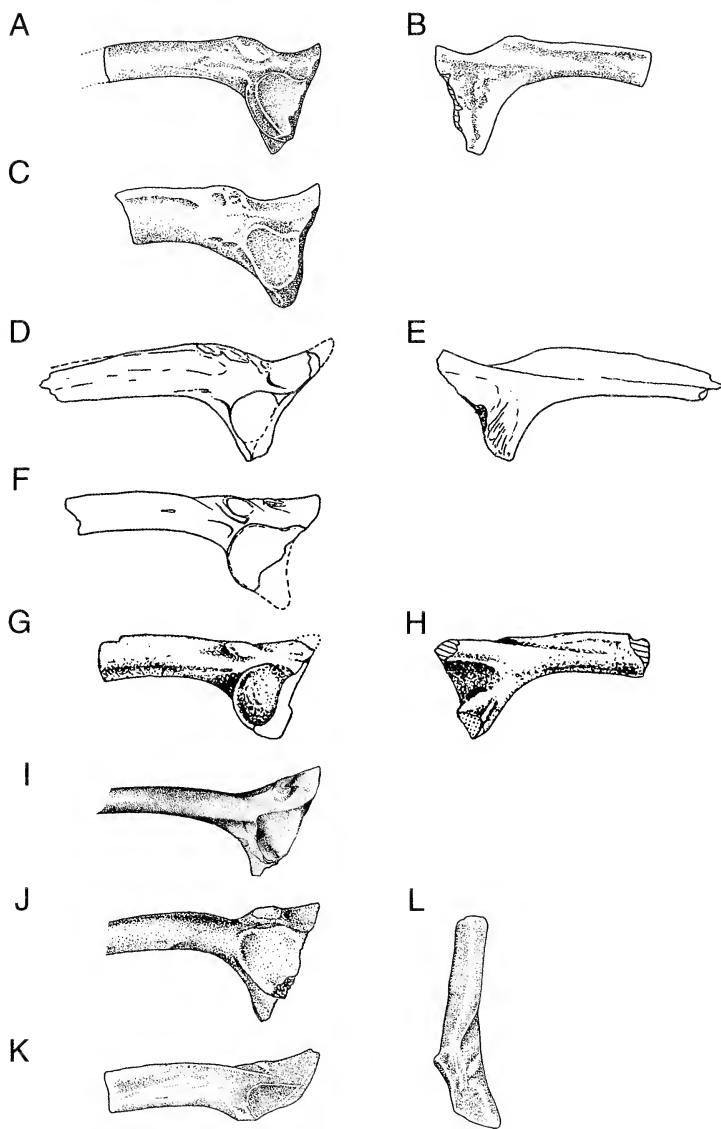


Fig. 16.—Comparison of iliac form in Anura. A–B, *Enneabatrachus hechti*, Upper Jurassic, North America, Discoglossidae, in A. Lateral, and B. Medial views. C, *Eodiscoglossus oxoniensis*, Discoglossidae, Middle Jurassic, England, lateral view. D–E, *Paradiscoglossus americanus*, Upper Cretaceous, North America, Discoglossidae, in D. Lateral, and E. Medial views. F, *Palaeobatrachus occidentalis*, Upper Cretaceous, North America, Palaeobatrachidae, in lateral view. G–H, *Pliobatrachus langhae*, Pleistocene, Romania, Palaeobatrachidae, in G. Lateral, and H. Medial views. I, *Scaphiopus alexanderi*, Miocene, North America, Pelobatidae, lateral view. J, *Tephrodytes brassicarvalis*, Oligocene, North America, Pelodytidae, lateral view. K–L, Pelobatoidea indet., Upper Jurassic, North America, in K. Lateral, and L. Posterior views. Figures not to scale. C, G–H, and K–L, have been reversed from the originals to aid comparison. (A–B, K–L, from Evans and Milner, 1993; C, from Evans et al., 1990; D–E, F, from Estes and Sanchíz, 1982b; G–H, from Sanchíz and Mlynarski, 1979; I, from Zweifel, 1956; J, from Henrici, 1994)

pelobatoids (Fig. 16I–L), however, in lacking the distinctive dorsal spiral groove (Evans and Milner, 1993; Henrici, 1994: seen most clearly in Fig. 16K–L). It further differs from that of living pipids in lacking the coossification of the pubis and ischium (although the juvenile condition of this has not been described) and in the possession of a rounded rather than elongate acetabulum (Trueb, 1996).

Jaw elements.—Most frogs have an abutting contact between the premaxilla and the maxilla, the two being held mostly by soft tissue, but pipimorphs (pipids and palaeobatrachids) share a derived condition (Trueb, 1973, 1993; Henrici, 1994, 1998*b*) whereby an edentulous process of the maxilla fits into a recess in the premaxilla. A similar condition occurs in some megophryine pelobatids (e.g., *Brachytarsophrys*, AMNH 23969; some species of *Megophrys*: *M. boettgeri*, AMNH 30361, and *M. lateralis*, AMNH 23549, but not *M. kuatunensis*, AMNH 30247: SE personal observation). Of the Anoual elements, the Type 1 maxilla and premaxilla show no evidence of a specialised articulation. They would be consistent with an attribution to the discoglossid or to any non-pipimorph frog. This conclusion is supported by the strong posterolingual process on the lamina horizontalis of the maxilla, a feature closely resembling that of the Tertiary genus *Latonia* (Roček, 1994). The Type 2 premaxilla, however, has a recess that matches the edentulous rostral part of the Type 2 maxilla. This configuration is not found in discoglossids and therefore the Type 2 elements may belong to *Aygroua*. Crown-group pipids are either edentate or have monocuspid acrodont teeth in which the pedicel has been lost (Trueb, 1996). Palaeobatrachids show the latter condition, while crown-group rhinophrynids are recorded as edentate (Trueb, 1973). However, the most basal rhinophrynid (*Rhadinosteus*, Henrici, 1998) retains bicuspid, pedicellate teeth, as does the Early Cretaceous pipimorph (contra pipid, Nevo 1968) *Thoraciliacus* (Trueb, 1999). The *Aygroua* maxilla and premaxilla therefore show a combination of character states consistent with those of a basal pipimorph.

Atlas.—Lynch (1971) described three atlantal types of which his ‘type II’ is generally thought to be the most primitive (e.g., Trueb, 1973), as it is found in archaic families (discoglossids, pelobatoids, rhinophrynids) and in the more primitive members of some neobatrachian lineages (e.g., ranids, bufonids, leptodactylids, Trueb, 1973). At Anoual, both atlantal morphotypes fit into this category, although the cotyles are more robust, rounded, and ventrally placed than those of most living anurans. The Anoual atlantes differ from one another in basic proportions (longer and narrower in Type 1) and the form of the posterior cotyle (wide and imperforate in Type 1). The Type 1 atlas is broadly similar to that of the discoglossids *Eodiscoglossus oxoniensis* (Middle Jurassic, Britain, Evans et al., 1990) and *E. santonjae* (Early Cretaceous, Spain, Estes and Sanchíz, 1982*b*), although the cotyles are more circular (Evans et al., 1990). The imperforate posterior cotyle suggests opisthocoely in successive vertebrae—a feature that would be consistent with attribution to discoglossids (see below). On this basis, Type 2 atlantes should be attributable to *Aygroua*, but show no features that specify their placement into one of the higher clades. The retention of a notochordal perforation in the posterior cotyle could be a primitive feature, or an immature configuration in a perichordal genus trending to either procoely (anomocoely) or ‘functional opisthocoely’ (sensu Estes, 1975) (as seen, for example, in juveniles of *Megophrys*, SE personal observation).

The atlas is discrete in all anurans except most crown-group pipimorphs, where it tends to fuse with the first post-atlantal vertebra. This occurs in known palaeobatrachids and in derived pipids (Trueb, 1996), and in many (but not all) specimens of the early (Early Cretaceous, Barremian) pipimorph *Thoraciliacus* (Trueb, 1999).

Post-atlantal presacral vertebrae.—The vertebral characters most frequently used in discussions of relationships amongst anurans are centrum type, central articulation, and

neural arch imbrication (e.g., Trueb, 1973). Griffiths (1963) recognized three developmental patterns for the vertebral centra—ectochordal, stegochordal, and holochordal. Ectochordy (today more often referred to as perichordy, e.g. Duellman and Trueb, 1986), in which the centrum develops as a cylinder around a central notochord, appears to be the primitive condition, but may also be the developmental condition from which the other types arise (Mookerjee, 1931). In stegochordy and holochordy, the centra are solid (depressed in stegochordy and rounded in holochordy). Basal living frogs (*Ascaphus*, *Leiopelma*), and early fossil taxa such as *Prosalirus*, *Vieraella* and *Notobatrachus*, have perichordal vertebrae (Trueb, 1973; Báez and Basso, 1996; Shubin and Jenkins, 1995), and this was clearly the primitive condition. However, perichordy is also present in rhinophrynids (Trueb, 1996; Henrici, 1998b), in the early pipoid *Thoraciliacus* (Nevo, 1968; Trueb, 1999), and in *Eodiscoglossus* (Estes and Sanchíz, 1982a; Evans and Milner, 1993), although discoglossids and pipoids are generally characterized as stegochordal (Trueb, 1973). Whether this perichordy persists as a primitive feature or has been re-developed secondarily through pedomorphosis (Green and Cannatella, 1993) is unclear, but it shows that the presence of perichordy must be treated carefully in phylogenetic discussions.

Both Anoual vertebral types are amphicoelous and notochordal, suggesting perichordal development. This is problematic with respect to Type 1 centra since living discoglossids show epichordal (stegochordal) development (Griffiths, 1963; Púgener and Maglia, 1997), and this should not involve a perichordal stage. However, Type 1 presacral centra are closely similar to isolated centra attributed to the Jurassic-Cretaceous genus *Eodiscoglossus*, both in their overall morphology and the slight dorso-ventral compression (Estes and Sanchíz, 1982a; SE personal observation). Either *Eodiscoglossus* is not a discoglossid (see discussion below of discoglossid relationships), or the patterns of vertebral development were not as clear-cut in the early stages of anuran evolution. Type 1 specimen MCM 207 (Fig. 7G–I) clearly shows that one of the Anoual frogs had opisthocoelous vertebrae with a basically perichordal pattern of development. Type 2 centra are more cylindrical and most closely resemble those of the Jurassic rhinophrynid *Rhadinosteus* (Henrici, 1998b; SE personal observation), the extant *Rhinophrynus dorsalis* (SE personal observation), and juveniles of some pelobatoids (e.g., *Megophrys monticola*, AMNH 24786).

With respect to the articulations between centra, amphicoely is recognized as the primitive anuran condition (e.g., *Triadobatrachus*, *Czatkobatrachus*, ascaphids, presacrals of *Eodiscoglossus oxoniensis*, SE personal observation) but can also occur in juveniles of other groups. Opisthocoely is found in most discoglossids, in basal pipimorphs such as *Thoraciliacus* (Trueb, 1999), and in living pipids and rhinophrynids; procoely is known in palaeobatrachids, some pelobatoids, and advanced (neobatrachian) frogs. Thus although the opisthocoelous/amphicoelous Type 1 Anoual vertebrae could belong to either the discoglossid or, potentially, *Aygroa*, the procoelous/amphicoelous Type 2 vertebrae cannot belong to the discoglossid and are more parsimoniously attributable to *Aygroa*. Trueb (1973) restricted true procoely to vertebrae having holochordal (neobatrachians and some pelobatids), rather than stegochordal or perichordal centra (palaeobatrachids, pelodytids). In pelobatoids (e.g., *Megophrys*, SE personal observation), but also rhinophrynids, the intervertebral disc remains unfused to the centrum for at least part of the life history (Trueb, 1973), thus the presacrals are either amphicoelous throughout life, or amphicoelous in the juvenile and procoelous or opisthocoelous in the adult (anomocoelous, Trueb, 1973). It seems likely that a cylindrical perichordal vertebral centrum is primitive for mesobatrachians, and therefore also basal pipoids (Trueb, 1996), with the intercentral discs attaching either to the front or to the back of adjacent centra. In their

combination of perichordy, immature amphicoely, and adult procoely, the Type 2 vertebrae appear most consistent with attribution to either a primitive pelobatoid or a primitive palaeobatrachid (assuming the basal pipimorph condition to be perichordy).

Both Anoual vertebral types have weakly imbricating neural arch laminae—a condition that is widespread in basal frogs (discoglossids, some pipoids, some pelobatoids including pelobatines and rhinophrynids) and a smaller number of neobatrachians (e.g., dendrobatids, microhylids, Trueb, 1973). The presence of fused ribs on the transverse process of MCM 78 would be consistent with either a discoglossid or a primitive mesobatrachian (Trueb, 1973), although the shape of the process matches that of the Type 1 (?discoglossid) vertebrae.

Sacral vertebrae.—Only two phylogenetically useful characters have been described for the sacral vertebra—the shape of the transverse processes and the nature of the sacro-urostyler articulation (Emerson, 1979, 1982).

Sacral transverse processes are described as expanded (some basal frogs, many neobatrachians), very expanded (particularly pipids and some pelobatoids) or cylindrical (principally ranids, but also some fossil discoglossids). None of the Anoual sacra have complete processes, but those of Type 1 appear stout and cylindrical (similar to those in described discoglossids such as *Wealdenbatrachus*, *Eodiscoglossus santonjae*, Sanchíz, 1998) while those of Type 2 are dorso-ventrally flattened and show a slight distal expansion (but less so than in *Thoraciliacus*).

In *Ascaphus* and *Leiopelma*, a pad of fibrocartilage connects the sacrum and urostyle, forming a synchondrosis. Since this is similar to the structure of a typical intervertebral joint, it is probably the primitive condition. A bicondylar joint develops in a majority of crownward anuran lineages including discoglossids, rhinophrynids, and myobatrachids, but the bones fuse in pipids, and either fuse or develop a monocondylar joint in pelobatoids. In *Thoraciliacus*, the articulation is monocondylar (Trueb, 1999). On this basis, the bicondylar Anoual Type 1 sacrum could belong to one of a number of anuran families (including discoglossids), but would be incompatible with most pipids or pelobatoids (although exceptions occur); its anterior condyle, however, is most suggestive of a discoglossid since it implies the bicondylar state combined with opisthocoely. In fact, the short, wide Anoual Type 1 sacral, with its large zygapophyses and broad transverse processes closely resembles that figured for *Wealdenbatrachus* (Early Cretaceous, Spain, Fey, 1988), allowing for the more posteriorly oriented processes of that genus. Although rhinophrynids are also 'functionally opisthocoelous' (Estes, 1975), the intervertebral disc does not fuse to the vertebral body and macerated vertebrae appear amphicoelous (Henrici, 1998b, SE personal observation).

The Type 2 sacrum is different. The well-defined pitted posterior recess probably held a pad of fibrocartilage, suggesting either a primitive synchondrosis or a step towards fusion/monocondyly. Without a detailed account of the developmental stages in fusion and monocondyly for various groups, it is difficult to judge.

Palaeobatrachid frogs show a tendency (*Palaeobatrachus*, *Pliobatrachus*) towards fusion of the sacral vertebra with one or more of the preceding presacrals to form a synsacrum (Špinar, 1972). In contrast, many pipoids (Trueb, 1996) and pelobatoids (e.g., *Pelobates*, *Megophrys*, SE personal observation) fuse the sacrum and urostyle, while incorporating one or more postsacrals (as shown by the presence of distinct spinal nerve foramina). There is no evidence that fusions of either type occurred amongst the Anoual frog material.

Urostyles.—Apart from the sacro-urostyler joint, the presence or absence of transverse processes is the only consistent urostyler character to be discussed. Transverse processes are retained in several basal frog lineages—*Ascaphus*, *Leiopelma*, discoglossids and

pelobatids, with the condition in pipids, leptodactylids, and bufonids considered variable (Trueb, 1973). Transverse processes are absent in the Jurassic *Notobatrachus* (Baéz and Basso, 1996), but present in the basal pipimorph *Thoraciliacus* (Trueb, 1999). The retention of transverse processes on all Anoual urostyles supports their attribution to basal or mesobatrachian frog lineages.

Pectoral girdle and forelimb.—No consistently applicable humeral or radioulna characters have been identified, except for the derived enlargement of the distal humeral condyle (greater than 60% of the overall distal humeral width, Báez and Basso, 1996; Gao and Wang, 2001). There are, however, features of the scapula that may be useful in discussion. A short stocky scapula is found in most primitive anurans and pipimorphs (Trueb, 1973). The scapula of *Rhinophrynus* and pelobatoids is 2–3 times longer than wide. In pipids, the blade is short (but probably secondarily so, Cannatella and Trueb, 1988), and shows fusion of the clavicle to the scapula. The scapula is proximally cleft in most lineages (except *Ascaphus*, some *Leiopelma*, most pipids), although the depth and orientation of the cleft varies. A direct medio-lateral cleft appears to be primitive (e.g., *Czatobatrachus*, *Eodiscoglossus oxoniensis*, *Prosalirus*), an oblique cleft—anterolateral to posteromedial—is more derived (e.g., *Rana*) (Borsuk-Bialynicka and Evans, 2002).

The two Anoual scapula morphotypes differ principally in their relative lengths, in the orientation of the scapular cleft, and in the presence (Type 2) of a crest or lamina along the anterior margin of the scapula (a pelobatoid character, Henrici, 1994, although in these taxa the crest typically runs the entire length of the scapula blade). The short, broad Type 1 scapula would be consistent with most basal frogs except *Ascaphus* and the derived pipids that lack a scapular cleft (*Leiopelma* shows variation, Sanchíz, 1998); the mediolateral orientation of the cleft suggests a basal rather than a derived frog. This type would therefore be consistent with attribution to a discoglossid and broadly resembles the scapula described for *Eodiscoglossus oxoniensis* (Evans et al., 1990). If this is correct, then the Type 2 scapula should belong to *Aygyroua*. It is longer and relatively narrower, with an oblique cleft and an anterior crest. This scapula type most closely resembles that of pelobatoid frogs and rhinophrynids (Henrici, 1994; SE personal observation), although in the latter group, the scapular cleft is medio-laterally oriented rather than oblique. The anterior crest is variable in its degree of development. In pipimorphs, including *Thoraciliacus* (Trueb, 1999), the scapula is shorter and also wider along its suprascapular margin. The scapula remains cleft in *Thoraciliacus*, but loses the cleft in the extant genus *Pipa*, supposedly in relation to its strong aquatic specializations (Trueb, 1973, 1996). The morphology of the Type 2 scapula is thus consistent with attribution to a mesobatrachian frog, but the combination of character states is problematic.

CONCLUSIONS

Introduction.—The fragmentary frog remains from Anoual demonstrate the presence of two distinct taxa. The presence of opisthocoeleous and procoeleous vertebrae respectively place these frogs above the level of *Ascaphus* and *Leiopelma* (and thus also of *Vieraella*, *Notobatrachus*, and *Prosalirus*), while the combination of perichordal vertebrae and transverse processes on the urostyles make neobatrachian status less plausible. Of the two Anoual taxa, one shows affinity to discoglossids, while the other appears to be a mesobatrachian.

Enneabatrachus.—The attributed ilia are closely similar to those of early discoglossids, particularly the Jurassic *Eodiscoglossus oxoniensis* (Evans et al., 1990) and *Enneabatrachus hechti* (Evans and Milner, 1993). They are tentatively referred to *Enneabatrachus*. One group (Type 1) of supplementary elements is also consistent with this interpretation.

If correctly attributed, these elements suggest that the Anoual discoglossid had opistho-coelous vertebrae (but with either primitive or paedomorphic perichordal development), with weakly imbricate vertebral neural arches, fused ribs on at least some vertebrae, a bicondylar sacrum, and a short, broad, mediolaterally cleft scapula.

The monophyly of Discoglossidae remains contested (e.g., Ford and Cannatella, 1993; but see Clarke, 1988; Sanchíz, 1998; Gao and Wang, 2001). Several discrete lineages have been recognized: Alytinae (the living *Alytes*); Bombinatorinae (the living *Bombina* and *Barbourula*); and Discoglossinae (the living *Discoglossus* and a series of referred fossil taxa including *Eodiscoglossus*, *Latonia*, *Paradiscoglossus*, and *Wealdenbatrachus*); and, less certainly, Gobiatinae (Late Cretaceous frogs from Asia) (Sanchíz and Řöcek, 1996; Sanchíz, 1998). Ford and Cannatella (1993) split the living taxa between the Bombinatoridae and Discoglossidae, but place *Eodiscoglossus* in an unresolved trichotomy with Bombinatoridae and the ancestry of all other frogs (their Discoglossanura). Gao and Wang (2001), by contrast, recovered a clade comprised of *Eodiscoglossus*, *Bombina*, and *Barbourula* in combination with their Early Cretaceous *Callobatrachus* (Wang and Gao, 1999). This clade formed the sister group of *Discoglossus* + *Alytes*, within a monophyletic Discoglossidae. The Jurassic *Ennebatrachus* and the Late Cretaceous *Scotiophryne* are of uncertain position (Sanchíz, 1998), although *Ennebatrachus*, at least, has a general resemblance to *Eodiscoglossus oxoniensis*.

Aygroua.—The second frog has an ilium that is sufficiently distinctive to permit the recognition of a new genus. Its phylogenetic position is more problematic. The ilium of *Aygroua* is consistent with attribution to a pipimorph frog (sensu Ford and Cannatella, 1993) in several features including: the large interiliac synchondrosis and relatively narrow interiliac angle; the narrow iliac shaft; and the absence of a dorsal tuberosity, but development of a crest-like dorsal prominence. It differs from the ilium of all pelobatoids in the absence of the characteristic spiral groove (Evans and Milner, 1993; Henrici, 1994) and in the development of the interiliac tuberosity (also absent in rhinophrynids). Pipimorph attribution would also be supported by the strong maxillary/premaxillary overlap (with a well-developed edentulous anterior maxillary process), although this feature can occur, independently, in megophryine pelobatids. The vertebrae have a juvenile morphology consistent with that of mesobatrachian frogs (rounded perichordal centrum, amphicoely in juvenile) and an adult morphology (procoely) found in some pelobatoids, in palaeobatrachid pipimorphs, and in neobatrachians. The scapula, if correctly attributed, most closely resembles that of pelobatoids (long blade, anterior lamina present, Henrici, 1994) and, to a lesser degree, rhinophrynids.

One further genus merits brief consideration. Until recently, procoely was regarded as a derived condition within crown-group Anura. Gao and Wang (2001) have described a plausibly procoelous frog (*Mesophryne*) from the Lower Cretaceous of China. Their cladistic analysis places this new genus on the anuran stem, raising the possibility, as yet unconfirmed, that procoely arose repeatedly at different stages of anuran evolution. Nonetheless, *Mesophryne* differs substantially from *Aygroua* in details of the pelvic morphology (see above) and premaxillary-maxillary contact.

In summary, *Aygroua* shows two out of six characters listed by Henrici (1998b) as characterizing pipimorphs, namely the interiliac tuberosity and the maxillary/premaxillary overlap. A further three characters are unknown in *Aygroua* (long metapodials, ossified pubis, ribs present), while the sixth (teeth conical) is absent in *Aygroua* (pedicellate and bicuspid), but also in *Thoraciliacus* (pedicellate and bicuspid), classified as a basal pipimorph by Trueb (1999). *Thoraciliacus* shares the maxillary/premaxillary overlap with *Aygroua* and pipimorphs (although it is difficult to determine the degree of this overlap in *Thoraciliacus*). The two fossil taxa also resemble one another in retaining rounded

perichordal centra, at least in the juvenile, but differ in that while *Aygroa* develops towards procoely, *Thoraciliacus* becomes opisthocoelous. They also differ markedly in scapular morphology and in the shape of the sacral transverse processes (more greatly flared distally in *Thoraciliacus*).

Allowing for the fragmentary nature of the Anoual material, and the necessarily tentative nature of element attribution, the existing evidence suggests that *Aygroa* is a mesobatrachian frog allied either to basal pelobatoids, to basal pipimorphs, or to basal palaeobatrachids. If a basal pelobatoid, *Aygroa* would represent a stage either prior to the development of the dorsal spiral groove on the ilium or a reversal of this state, while the premaxillary/maxillary overlap and strong interiliac tuberosity would have been acquired independently (as in *Megophrys*). Interpretation as a basal pipimorph would be consistent with the overlapping premaxillary/maxillary contact and several pelvic features (see above), and would be unaffected by the retention of pedicellate, bicuspid teeth, but it would require that perichordy or anomocoely is primitive to the clade (a reasonable assumption given the condition in *Thoraciliacus*), with procoely or opisthocoely both possible. Attribution to a basal palaeobatrachid would be consistent with procoely, but would require that loss of pedicellularity had evolved independently in both pipids and palaeobatrachids, and that *Aygroa* represents a stage prior to the fusion of V1 and V2, fusion of the sacrum and posterior presacra, and reduction of the maxillary dentition (12–16 teeth in palaeobatrachids, Sanchíz, 1998). Loss of the bicondylar sacrum in *Aygroa* would be secondary.

Currently, the oldest recorded mesobatrachians are from the Upper Jurassic Morrison Formation of the U.S.A., with an indeterminate pelobatoid (Evans and Milner, 1993) and a pipoid (a possible basal rhinophrynid, Henrici, 1998b). Pipoids have also been recorded from the Lower Cretaceous of Israel (*Cordicephalus* and *Thoraciliacus*, Nevo, 1968; Trueb, 1999), while palaeobatrachids are first recorded with confidence from the Upper Cretaceous (Sanchíz and Roček, 1996; Sanchíz, 1998). The basal Cretaceous *Neusibatrachus* (Montsech, Spain) was referred to the Palaeobatrachidae by Seiffert (1972) and by Estes and Reig (1973). Sanchíz (1998) synonymised the taxon with *Eodiscoglossus santonjae* from the same locality, although Roček (2000) has queried this. The earliest confidently recorded neobatrachians are leptodactylids from the Late Cretaceous of Brazil (Báez and Peri, 1989).

Palaeobiogeographic implications

To date, living and extinct discoglossids, pelobatoids, rhinophrynids, and palaeobatrachids are limited to northern continents or to regions that have clearly been colonized from the north (e.g., India). Pipids may fill the niche of pelobatoids and palaeobatrachids in Southern continents (Gondwana, e.g., Báez, 1981, 1996), while neobatrachian frogs may also have evolved and radiated from the south (Duellman and Trueb, 1986). Although albumin studies have suggested an origin for pipoids at about 130 Ma (Bisbee et al., 1977), the evidence from the fossil record would place it earlier than this. Since rhinophrynids (Henrici, 1998b) and, apparently, pelobatoids (Evans and Milner, 1993) are recognized from at least the Late Jurassic (Kimmeridgian, ca. 145 Ma), their ancestors must have separated during or before the Middle Jurassic (ca. 160 Ma). The breakup of Pangea was occurring about this time (Bajocian–Callovian, ca. 170–160 Ma, Smith et al., 1994; Dercourt et al., 2000), and it is plausible that this divided the ancestral pipimorph stock, with pipids developing in Gondwana (e.g., Báez et al., 2000) and palaeobatrachids in Laurasia (Sanchíz and Roček, 1996); pelobatoids remained in Laurasia, and rhinophrynids may have evolved in North America (Duellman and Trueb, 1986).

Similar arguments cannot be applied to discoglossids, monophyletic or not, since they were apparently in existence by the Bathonian (Evans et al., 1990). However, following a theory proposed by Hallam (1975), Růček (2000) has suggested that an arid equatorial belt might have restricted the spread of discoglossids to southern continents in the Jurassic. This would not be contradicted by the presence of the group in northwest Africa, a region to the north of the arid belt.

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Appendix—Anatomical Terms and Abbreviations

ac—acetabulum
 ac.b—acetabular border
 a.ct—anterior cotyle
 a.lm—anterior lamina
 al.pr—alary process
 a.tb—anterior tubercle
 a.zy—anterior zygapophysis
 btt—buttress
 ce—centrum
 cr.cr—crista cruris
 cr.d—crista dorsalis (dorsal crest)
 cr.f—crista femoralis
 cr.pv—crista paraventralis
 cr.v—crista ventralis
 d.pr—dorsal prominence
 ed.rs—edentulous rostrum
 fs.cb—fossa cubitalis ventralis
 fs.h—fossa for humeral condyle
 fs.mx—fossa maxillaris
 g—gutter
 h.co—humeral condyle
 il.bl—iliac blade
 i.tb—interiliac tubercle
 l.cr—lateral crest
 l.gr—lateral groove
 lm.h—lamina horizontalis
 l.pt—ligament pit
 m.bt—medial buttress
 mx.f—maxillary facet
 n—notch
 n.f—nutrient foramen
 no.c—notochordal canal
 n.sp—neural spine
 ol—olecranon
 ol.s—olecranon scar
 p.ac—pars acromialis
 p.asc—processus ascendens (dorsal acetabular expansion)
 p.co—posterior condyle
 p.cor—processus coronoideus
 p.ct—posterior cotyle
 pd—neural arch pedicel
 p.den—pars dentalis
 p.des—processus descendens (ventral acetabular expansion)
 p.gl—pars glenoidalis
 p.pl—pars palatina
 pr.pl—processus palatinus
 p.zy—posterior zygapophysis
 r—radius
 r.e—raised edge
 rs—rostrum
 sc.bl—scapular blade
 s.int—interglenoid sinus

s.mk—sulcus for Meckel's cartilage
s.sc.s—attachment for suprascapular cartilage
tb—tubercle on premaxilla
tb.s—tuber superior (dorsal tubercle)
tr.pr—transverse process
u—ulna
u.ep—ulnar epicondyle
v.gr—ventral groove
w.ex—waisting then expansion

RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. XII.
FIRST RECORD OF THE GIANT FRUIT-EATING BAT, *ARTIBEUS AMPLUS*,
(MAMMALIA: CHIROPTERA) FROM SURINAME
WITH A REVIEW OF THE SPECIES

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ABSTRACT

Herein, we report new distributional records of *Artibeus amplus*, including its first documentation from Suriname, the southern-most records from Guyana, and the confirmation of its occurrence in the llanos savannahs of central Venezuela. This uncommon species is endemic to northern South America, and is one of the least known bats in the Neotropics. Additional ecological data are included in a review of information on natural history of this species. With the addition of *A. amplus* to the fauna, 104 species of bats are now known from Suriname.

KEY WORDS: *Artibeus amplus*, *Artibeus planirostris*, fruit-eating bats, Guyana, Suriname, Venezuela

INTRODUCTION

The giant fruit-eating bat (*Artibeus amplus*) is one of the most poorly known bats in the northern Neotropics. It is of particular interest, however, as one of the few species of bats endemic to northern South America, north of the Amazon River drainage basin. In his original description of the species, Handley (1987) reported 55 specimens from 10 localities in Venezuela and one locality in Colombia. Four of these were listed as “*Artibeus* sp. D.” in an annotated checklist of mammals from the Smithsonian Venezuelan Project (Handley, 1976:33).

There have been few subsequent reports of this species in the scientific literature. The exceptions, however, include 38 individuals of *A. amplus* netted between 28 March and 5 August 1987 from Los Pijiguaos in a montane forested area within the llanos savannah of central Venezuela (Ochoa G. et al., 1988). Unfortunately, these authors did not specify the number of voucher specimens prepared and the museum of deposition in Venezuela. More recently, Lim and Wilson (1993) reported 10 specimens from six localities in Guyana and quantified morphometric differences between *A. amplus* and other large species of *Artibeus*. In a monograph on the mammals of Venezuela (Linares, 1998), 12 collection localities were mapped for *A. amplus*. There was, however, no specimens examined list or gazetteer to cross-reference these localities. In that monograph, there were three localities in addition to those mentioned in Handley (1987), including an additional record for the state of Bolívar and what appear to be the first records for the states of Áchira and

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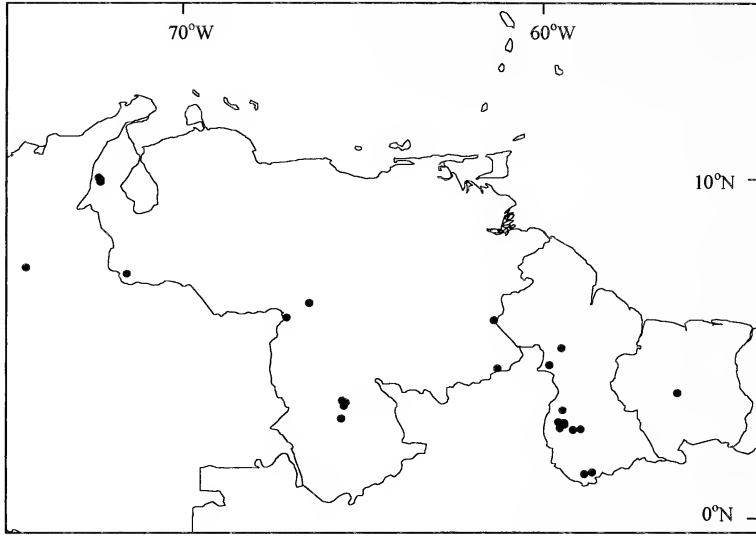


Fig. 1.—Map of northern South America with known locality records for *Artibeus amplus* from Colombia, Venezuela, Guyana, and Suriname. See “Specimens Examined” and Appendix 1 for locality details.

Portuguesa. We expand the known distributional range of *A. amplus* by documenting its first occurrence in Suriname, the southern-most record from the upper Essequibo River region of Guyana, and confirm its presence in the llanos of Venezuela. We also summarize the natural history of this species and provide information on its identification.

MATERIALS AND METHODS

Eleven cranial measurements were taken with digital callipers to the nearest 0.1 mm for the 10 new specimens of *A. amplus* reported in this study. The measurements were described in Lim and Wilson (1993) and include cranial length, palatal length, length of maxillary toothrow, breadth of zygomatic arch, mastoid breadth, width across upper molars, postorbital constriction, rostral length, interorbital width, width across upper canines, and coronoid height. External measurements were those recorded by the original collectors and included total length of body, length of hindfoot, length of ear, length of tragus, length of forearm, and mass (in g).

SPECIMENS EXAMINED

Locality information for the new specimen records, including country, region, locality, latitude, longitude, elevation (when known), and museum catalog number, is given below. Abbreviations are ROM, Royal Ontario Museum, and CM, Carnegie Museum of Natural History.

GUYANA. Upper Takutu-Upper Essequibo: Essequibo River, 7 km S Gunn's Strip, 240 m, 1°35'N, 58°38'W (ROM 106748, 106761). Kamoia River, 50 km SWW Gunn's Strip, 1°32'N, 58°50'W (ROM 106679, 106697, 106722). Sand Creek Village, 32 to 48 km down river, approximately 3°00'N, 59°31'W (ROM 70125). Weri More, Quash Wau area, 19 km NE Dadanawa, 2°56'N, 59°29'W (ROM 67311).

SURINAME. Saramacca: Center of Arrowhead Basin, Augustus Creek, Tafelberg, 600 m, 3°54'N, 56°10'W (CM 76795).

VENEZUELA. Amazonas: Pozon, 50 km NE Puerto Ayacucho, 6°03'N, 67°25'W (ROM 107847, 107904).

RESULTS AND DISCUSSION

The first specimen of *Artibeus amplus* from Suriname was obtained by Stephen L. Williams on 3 November 1981. It was a pregnant adult female with an embryo having a crown-rump length of 16 mm. This record is the eastern-most currently known for the species (Fig. 1). The collecting site was in the center of a large basin on the top of Tafelberg

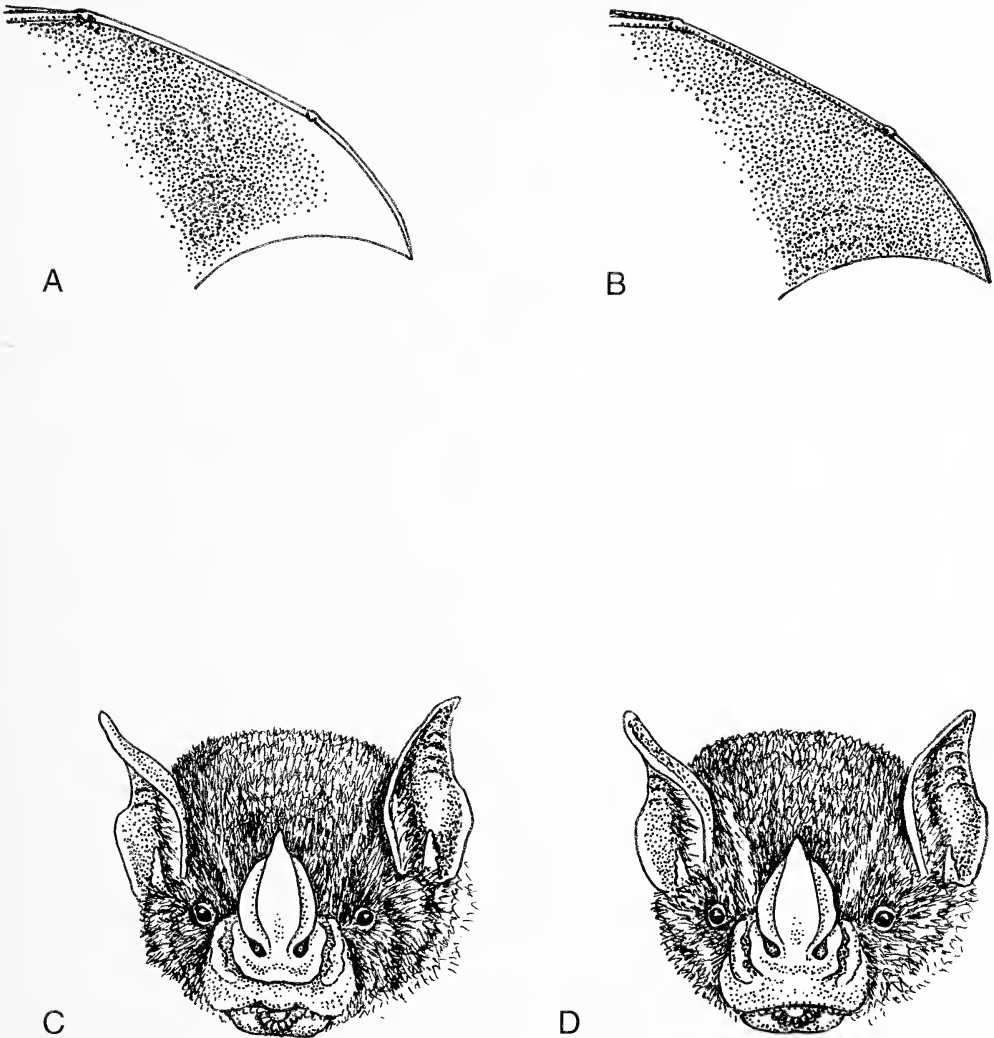


Fig. 2.—External differences between *Artibeus planirostris* and *A. amplus*. A. The white wing tip in *A. planirostris* contrasts with the brown color of the remainder of the wing; B. The wing tip in *A. amplus* is the same brown color as the remainder of the wing; C. The noseleaf in *A. planirostris* forms a complete margin of skin at the base, separating it from the upper lip; D. The base of the noseleaf in *A. amplus* merges continuously with the upper lip. Illustrations by Fiona A. Reid.

(600 m), which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guayana Crystalline Shield (Maguire, 1970).

Tafelberg is almost completely rimmed by vertical cliffs that rise over 300 m above the surrounding lowland tropical forest. Only in one area of the northwestern rim is there a breakdown area, allowing overland access to the mountaintop. The mountain is a tilted triangular block of sandstone that is highest at the narrow southern end and lowest along the broad northern escarpment. The principal topographic feature of the mountain is the Arrowhead Basin, which also is triangular in shape, but its orientation is the reverse of that of the mountain. At its broad southern end there is an escarpment wall about 180 m in

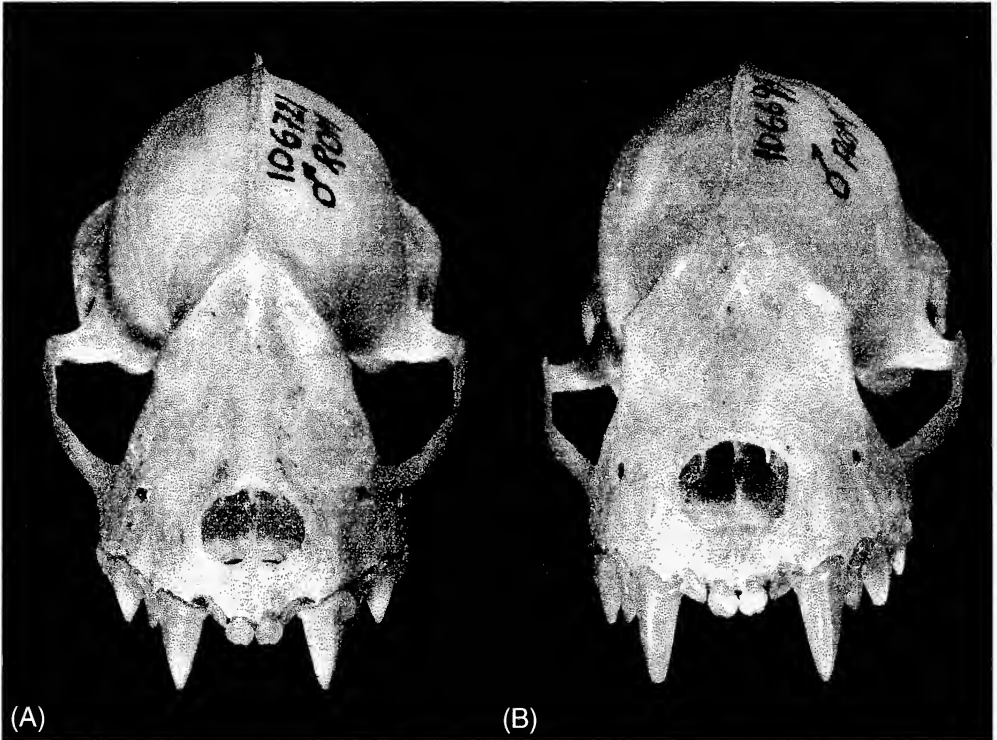


Fig. 3.—Cranial difference between *Artibeus planirostris* and *A. amplus*. A. The orbitorostral shield converges posteriorly towards the postorbital processes in *A. planirostris*; B. The lateral edges of the orbitorostral shield are nearly parallel posteriorly towards the postorbital processes in *A. amplus*. Photography by James Knowles.

height over which several small streams form waterfalls that collect in the basin to form Augustus Creek.

Maguire (1945a, 1945b, 1970) and Maguire et al. (1953) described the vegetation of Tafelberg as complex and related to the flora of the Guayana Highlands. Most of the top of the mountain is dominated by intermediate tropical bush; however, low areas including the Arrowhead Basin are dominated by high forest. In the basin, the forest is dominated by dakama (*Dimorphandra* sp.) with large buttressed roots and forming a dense canopy that allowed only filtered light to reach the ground.

On the evening that the specimen of *A. amplus* was captured, mist nets were placed across Augustus Creek in an area with a dakama forest canopy and over a seasonally dry pond in a forest opening. Over 90 linear meters of mist nets were used during the night. Only three other species were taken during the night, with each represented by a single specimen—*Pteronotus parnellii*, *Rhinophylla pumilio*, and a small species of *Eptesicus*. On the previous evening in this same area, two specimens of *Artibeus obscurus* were netted.

Specimens representing the southern-most records for the species were collected by Burton K. Lim, Eamon O'Toole, and Charles J. Robertson in the vicinity of the Wai-Wai village of Gunn's Strip in southern Guyana. The general habitat was tall evergreen non-flooded hill-land forest (Huber et al., 1995). Three were caught near a landing on the Kamoa River about 2 km from the base of the Kamoa Mountains. An adult male with testes measuring 3 by 2 mm was taken around 2130 h on 9 November 1996 in a mist net

Table 1.—*External measurements (mm) of 10 new specimens and previously reported samples of Artibeus amplus from northern South America.*

Catalog number and/or country	Total length	Hind foot length	Ear length	Tragus length	Forearm length	Mass (g)
CM 76795						
Suriname	96	21	26	—	69	60
ROM 67311						
Guyana	90	—	23	9	67	—
ROM 70125						
Guyana	86	—	25	9	71	—
ROM 106679						
Guyana	91	20	22	7	71	50
ROM 106697						
Guyana	93	19	23	8	65	47
ROM 106722						
Guyana	99	20	21	7	72	56
ROM 106748						
Guyana	92	20	22	7	68	46
ROM 106761						
Guyana	93	19	23	7	68	52
ROM 107847						
Amazonas, Venezuela	97	20	23	8	72	57
ROM 107904						
Amazonas, Venezuela	94	19	23	8	68	58
Colombia, Guyana, and Venezuela ¹	—	—	—	—	69.5 (64.9–73.4)	—
Zulia, Venezuela, and Colombia ²	100.4 (93–104)	18.4 (17–19)	23.7 (22–26)	—	70.8 (68.6–75.3)	—
T. F. Amazonas and Bolivar, Venezuela ²	89.9 (80–100)	18.3 (17–20)	23.0 (18–26)	—	69.1 (65.0–73.2)	—

¹ Lim and Wilson, 1993.

² Handley, 1987.

set across a newly cut trail in the forest understory (<3 m above the ground) within 200 m of the landing. A non-reproductive adult female was captured early in the morning on 14 November 1996 in a mist net placed further along the trail near the base of the mountain. An adult male, with testes measuring 9 by 5 mm, was obtained at approximately 2030 h on 11 November 1996 in a net set along a tree fall into the Kamo River. Two additional specimens were collected near a landing on the Essequibo River at a point 7 km south of Gunn’s Strip (240 m elevation). A non-pregnant adult female was caught around 2030 h on 16 November 1996 and an adult male with testes measuring 10 by 7 mm was caught in the early morning on 20 November 1996. Both were captured in the same mist net placed across a newly cut forest trail near a stream crossing.

Two additional specimens recently were discovered in the Guyana collections amassed from 1961 to 1975 by Randolph L. Peterson at the Royal Ontario Museum (ROM), and not reported in Lim and Wilson (1993). Both were collected by Jerome Marques in the southern Rupununi region. An adult female was obtained between 20 October and 15 November 1972 in forest edge at the foot of the Kanuku Mountains. An adult male was netted in primary rainforest at Weru More in 1973 sometime prior to its deposition at the ROM in November of that year.

Two specimens were collected in the llanos region of central Venezuela near the Orinoco River and the Colombian border by Burton K. Lim, Thomas E. Lee, Jr., and John

Table 2.—Cranial measurements (mm) of 10 new specimens and previously reported samples of *Artibeus* amplus from northern South America.

Catalog number and/or country	Cranial length	Palatal length	Maxillary toothrow length	Zygomatic breadth	Mastoid breadth	Breadth across upper molars	Postorbital constriction	Rostral length	Interorbital width	Width across upper canines	Coronoid height
CM 76795 Suriname	31.2	12.2	11.1	18.2	15.5	13.5	7.9	14.6	9.0	8.4	7.7
ROM 67311 Guyana	30.2	12.0	10.7	18.5	15.9	13.4	7.5	13.4	9.1	8.5	7.7
ROM 70125 Guyana	31.3	12.4	10.8	18.6	16.6	13.2	7.7	14.4	9.5	8.7	8.4
ROM 106679 Guyana	31.5	12.4	11.0	18.3	16.4	12.9	7.7	14.6	9.1	8.6	8.5
ROM 106697 Guyana	30.9	12.5	11.0	17.7	15.8	13.3	7.9	14.2	9.4	8.9	8.2
ROM 106722 Guyana	31.1	12.0	10.9	18.2	16.3	13.1	7.7	14.3	9.2	8.6	8.6
ROM 106748 Guyana	30.7	12.2	10.8	17.3	16.1	12.6	7.8	14.0	8.5	8.2	8.2
ROM 106761 Guyana	31.3	12.5	11.5	18.5	15.6	13.7	8.3	14.1	9.5	9.1	8.8
ROM 107847 Amazonas, Venezuela	31.4	12.6	10.8	18.8	15.9	13.4	7.7	14.8	9.2	8.8	8.8
ROM 107904 Amazonas, Venezuela	30.7	12.9	10.9	17.8	16.2	13.2	7.9	14.2	9.5	8.8	8.5
Colombia, Guyana, and Venezuela ¹	31.6 (30.5–33.2)	12.6 (11.8–13.4)	11.3 (10.8–11.9)	18.4 (17.9–19.1)	16.2 (15.4–17.1)	13.4 (12.9–13.9)	7.9 (7.4–8.4)	14.6 (13.6–15.8)	9.3 (8.4–10.2)	8.9 (8.4–9.6)	8.5 (7.7–9.0)
Zulia, Venezuela, and Colombia ²	31.4 (31.0–31.9)	– (11.1–11.5)	11.2 (11.1–11.5)	18.6 (18.1–18.8)	–	13.2 (12.7–13.5)	7.9 (7.6–8.3)	–	–	8.4 (8.2–8.8)	–
T. F. Amazonas and Boilvar, Venezuela ²	31.2 (30.3–32.8)	– (10.7–11.8)	11.2 (10.7–11.8)	18.4 (17.4–19.1)	–	13.3 (12.8–13.9)	7.8 (7.3–8.4)	–	–	8.6 (8.3–8.9)	–

¹ Lim and Wilson, 1993.² Handley, 1987.

D. Hanson. The general habitat was savannah with granite outcrops, forested hills, gallery forest, and other scattered patches of forest (bush islands). An adult non-reproductive female was taken on 21 July 1997 in a mist net placed in the forest near an intermittent creek at the base of a hill. An adult male with testes measuring 5 by 3 mm was caught in a mist net set across a dirt road passing through a stand of trees on 25 July 1997.

Although not widely distributed or relatively abundant, the ecological range of *A. amplus* is quite varied. Originally, it seemed to be closely associated with forested montane habitats. Only four specimens from two localities (Nulita and Tamatama) in the type description were lowland rainforest sites (Handley, 1987). The species subsequently was caught in the llanos savannah of Venezuela but still in close association with montane forest (Ochoa G. et al., 1988). However, in the first report of *A. amplus* from Guyana, the species was found in more typical dry savannah habitats at Dadanawa and Shea Village (Lim and Wilson, 1993). In this study, we also caught this bat during the wet season from gallery forest and bush islands in the llanos savannah of Venezuela. *Artibeus amplus* now has been taken in montane forest (1200 m), lowland forest (24 m), and savannah, with gallery forest or bush islands. The only known roosts for *A. amplus* are caves (Handley, 1987), but it probably also roosts in trees like other larger species of *Artibeus* (Emmons, 1997).

As outlined by Handley (1987), there are several external and cranial characters that distinguish *A. amplus* from the similar-sized *A. planirostris*. The tips of the wings of *A. amplus* are brown, and not white as seen in *A. planirostris*; and the noseleaf in *A. amplus* does not form a complete margin of skin at the base as does *A. planirostris*, but instead merges continuously with the upper lip (Fig. 2). In addition, the orbitorostral region of the skull in *A. amplus* is more robust with the lateral edges nearly parallel from the rostrum posteriorly towards the postorbital processes, as opposed to converging (Fig. 3). The skull is also proportionally longer and narrower (see Lim and Wilson, 1993).

The external and cranial measurements of the 10 new specimens from six localities are presented in Tables 1 and 2. The new specimens compare favorably in their measurements with those reported in Handley (1987) and Lim and Wilson (1993). The specimen from Suriname, however, had a relatively long hind foot and the highest recorded mass, although it was a pregnant female. One noteworthy observation about the mensural data for *A. amplus* is their relative uniformity across a broad geographic range from Colombia to Suriname in northern South America.

Artibeus amplus is now known by approximately 116 specimens from 27 localities in northern Colombia, Venezuela, Guyana, and central Suriname (Fig. 1). This distribution is unique in that it includes the Guianan subregion of Amazonas, eastern slopes of the northern Andes, and North Coast faunal provinces for bats (Koopman, 1976, 1982). The only other species of bat that has a similar distributional range is the even more enigmatic *Micronycteris homezi* (see Simmons and Voss, 1998; Lim and Engstrom, 2001). The distribution and abundance of these two previously unrecognized cryptic species may be underestimated in museum collections, or have gone undetected in trap-and-release ecological studies. Based on our current knowledge, however, each is restricted to non-Amazonian drainage to the north Atlantic coast of South America. The addition of *A. amplus* to the fauna of Suriname brings the known bat diversity in this country to 104 species (see Lim and Engstrom, 2001).

ACKNOWLEDGMENTS

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through a grant to the Section of Mammals of the Carnegie Museum of Natural History. Mr. Henry A. Reichart, STINASU, assisted our research in many ways and made facilities of STINASU available for our use. Ferdinand L. J. Baal, Department of Forestry, issued our collecting permits. Fieldwork in Guyana was funded by the Biological Diversity of the Guianas program at the Smithsonian Institution, and the Centre for Biodiversity and Conservation Biology, Royal Ontario Museum. Research and export permits were facilitated by the Centre for the Study of Biological Diversity at the University of Guyana, Ministry of Amerindian Affairs, and the Environmental Protection Agency. Funding for research in Venezuela was made possible with the generous assistance of the Peterson Memorial Fund of the ROM Foundation, and the Centre for Biodiversity and Conservation Biology, ROM. Daniel Lew, Museo de Historia Natural La Salle, assisted with the permits issued by Servicio Autónomo Profauna. Thanks to Fiona Reid for the illustrations of the external characters and to James Knowles for the photograph of the skulls. This is contribution number 256 from the Centre for Biodiversity and Conservation Biology at the Royal Ontario Museum.

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Appendix 1—Additional Locality Records for *Artibeus amplus*.

Specimens from Colombia and Venezuela were records reported in Handley (1987), unless noted with * (Ochoa G. et al., 1988), and those from Guyana were reported in Lim and Wilson (1993). Three Venezuelan localities plotted by Linares (1998) were not included because specimens, exact localities, and latitude and longitude were not presented.

COLOMBIA. Antioquia: La Tirana, 33 km SW Zaragoza, 520 m, 7°30'N, 74°52'W.

GUYANA. Potaro-Siparuni: Kaieteur Falls, 5°10'N, 59°29'W. Kato, Chiung River, 4°40'N, 59°49'W. **Upper Takutu-Upper Essequibo:** Dadanawa, 2°50'N, 59°31'W. Kuitaro River, 48 km E Dadanawa, approximately 2°50'N, 58°57'W. Nappi Creek, Kanuku Mountains, 40 km E Lethem, 3°23'N, 59°28'W. Shea Village, Kumakowri River, 2°49'N, 59°09'W.

VENEZUELA. **Amazonas:** Belén, Río Cunucunuma, 56 km NNW Esmeralda, 150 m, 3°39'N, 65°46'W. Cabecera del Caño Culebra, Cerro Duida, 40 km NNW Esmeralda, 1140–1200 m, 3°30'N, 65°43'W. Caño Culebra, Cerro Duida, 50 km NNW Esmeralda, 800 m, 3°37'N, 65°41'W. Tamatama, Río Orinoco, 2 km above Boca del Casiquiare, 135 m, 3°10'N, 65°49'W. **Apure:** Nulita, Selvas de San Camilo, 29 km SSW Santo Domingo, 24 m, 7°19'N, 71°57'W. **Bolívar:** 21 to 33 km NE Icabarú, 775–851 m, 4°35'N, 61°19'W. Km 125, 85 km SSE El Dorado, 826–1165 m, 5°59'N, 61°26'W. *Serranía de Los Pijiguaos, approximately 140 km SW Caicara del Orinoco, approximately 6°29'N, 66°43'W. **Zulia:** Kasmera, 21 km SW Machiques, 270 m, 9°59'N, 72°43'W. 15 km W Machiques, approximately 10°05'N, 72°43'W. Novito, 19 km WSW Machiques, 1135 m, 10°02'N, 72°43'W.

FROM THE ARCHIVES AND COLLECTIONS

C. V. HARTMAN'S LETTER OF MAY 27, 1907 TO C. C. MELLOR

DAVID R. WATTERS¹OSCAR FONSECA ZAMORA²

THE CONTEXT OF THE LETTER

Carl Vilhelm Hartman had served as a Curator at Carnegie Museum for four years and three months when he wrote this lengthy letter to Charles Chauncey Mellor, Chair of the Museum Committee of Carnegie Institute. Director W. J. Holland had hired Hartman as the Curator of Ethnology and Archaeology on February 28, 1903. He reported for duty on March 17, departed less than two weeks later for Costa Rica on the Carnegie Museum expedition, and returned to Pittsburgh in November. In succeeding years, he headed the Section of Ethnology and Archaeology, administered the "Annex facility" that housed the Section until January 1907, researched and published the Costa Rican artifacts he had obtained, and installed the anthropology exhibits in the newly enlarged Carnegie Institute building that was dedicated in April 1907 (Watters and Fonseca Zamora, 2002*a*, 2002*b*).

The primary objective of Hartman's letter was to obtain an increase in his salary. His salary (monthly \$166.66; annually \$2000) in 1907 was exactly the same as when he was hired in 1903 despite more than four years of dedicated service. Hartman wrote this well-organized, carefully crafted letter in order to enumerate his accomplishments since joining Carnegie Museum. To bolster his case, he documents his service to the Museum, explains the contexts of his achievements, and reviews his communications with Holland. This letter to Mellor is the sole source of information about some aspects of his accomplishments; other points can be corroborated by documents in the Hartman Archives at Carnegie Museum of Natural History. The Mellor letter contains the most forthright statement and detailed listing of what Hartman perceived to be his significant contributions at Carnegie Museum through May 1907. He also devoted major sections of the letter to his achievements before coming to Carnegie Museum.

By addressing the letter to the Chair of the Museum Committee, Hartman bypassed the Director, and this decision reflected their increasingly strained relationship, an estrangement beginning during the 1903 expedition. Documents in the Holland Archives give the Director's perspectives on the context of this letter and the larger issue of compensation of staff at Carnegie Museum. Hartman did not act alone. The Holland Archives disclose that Mellor received a second letter, also requesting a salary increase, written by Arnold E. Ortmann, Curator of Invertebrate Zoology. The Museum Committee's receipt of both letters is recorded in the Minutes of its May 31 meeting. The timing of the two letters, occurring soon after the dedication of the expanded Carnegie Institute facility in April,

¹ Curator, Section of Anthropology.

² Research Associate, Section of Anthropology (and Professor, retired, University of Costa Rica). Submitted 26 December 2002.

when staff members were becoming more vocal about postponed raises, assuredly was not happenstance.

THE CONTENT OF THE LETTER

Hartman's original letter on Section of Ethnology and Archaeology printed letterhead is twenty pages long, typed double-spaced, and contains a few hand-written additions and corrections. The letter's text is reproduced below in its entirety. It has been edited only for minor points, such as eliminating extra spaces between words and before periods and commas. We have inserted a bracketed *sic* for original typographical and grammatical errors, a bracketed notation indicating the end of each original text page, and bracketed passages when explanatory text is necessary. Hartman's spelling idiosyncrasies (e.g., archeology, characterised) are retained and his diacritical marks, which he added by hand, are reproduced as originally presented, even though he was not consistent in their use (e.g., San José and San Jose, Sjögren and Sjogren, Fabrrega and Fabrega).

We segregate blocks of text within the letter, usually comprising a set of paragraphs related contextually. Appearing at the end of each block of text is our commentary that clarifies meaning and provides context. We consecutively numbered the original fifty paragraphs (inserting bracketed numbers in front) to associate our comments with the individual paragraph and to facilitate our discussion about related textual materials that occur in noncontiguous paragraphs. Hartman quoted a number of writings at length, and we have indented these block quotations to distinguish them from paragraphs he wrote.

CARNEGIE MUSEUM

(SECTION OF ETHNOLOGY AND ARCHÆOLOGY)

C. V. Hartman, Curator.

PITTSBURGH, PENNSYLVANIA, U. S. A.

May 27, 1907.

Mr. C. C. Mellor,
Chairman of the Museum Committee,
Carnegie Institute, City.

Dear Sir:—

[1] I hereby take the liberty of addressing you, asking you to kindly lay before the Committee, of which you are the Chairman, the following respectful request for a regulation and increase of my salary as Curator of the Section of Ethnology and Archeology. The reasons which I consider might entitle me to the consideration of a raise of salary now, when entering the beginning of the fourth year of my service, I will here state, asking your indulgence for the rather lengthy recital of details involved.

[2] In March 1903 I was appointed by your Committee as Curator of the Section. After a few days hasty preparation I left, via New Orleans, for Costa Rica, in order to realize an old plan of mine, which had met the hearty approval of the Director, to carry out certain archeological investigations and procure for the Carnegie Museum some valuable collections, known and investigated by me during my previous expedition to that country under the auspices of the Swedish Ethnographical Museum. [end of page 1 of original document]

Paragraph 1 sets forth Hartman's primary reason for writing the letter. Despite the statement in paragraph 2, Hartman and Holland signed the hiring document not in March but on February 28, 1903, the very day the Museum Committee approved the Director's recommendation (Watters and Fonseca Zamora, 2001b). Hartman first wrote Holland on January 28, discussing at length his "old plan" to resume archaeological research in Costa Rica, and in Spanish America in general. However, Holland already was aware of Hartman's Costa Rica research on the earlier (1896–1899) Swedish expedition, for he had

heard him lecture about it three months earlier, in October 1902, at the 13th Session of the International Congress of Americanists in New York City (Watters, 2002). When Hartman left Pittsburgh (probably on March 25) to begin the Carnegie Museum expedition, he traveled by train to Cincinnati and New Orleans, where he took passage on the United Fruit Company's steamship *Preston* for the onward trip to Puerto Limón, Costa Rica. He had boarded the vessel by March 27, the day he posted a letter to Carnegie Museum using *Preston* letterhead. The date he arrived in Costa Rica is not known.

[3] According to the written instructions given me, I had first of all to proceed to San José, the capital, in order to purchase the famous Velasco collection of antiquities, since some time deposited by the owner in a Philadelphia museum. For said collection I was authorized to apy [sic] a sum not exceeding \$3000. Verbally I was told, that I, if necessary, could pay \$500 more, but in such a case I ought first to notify the Director.

[4] Regarding the expenses during my adjournment in Costa Rica, the Director informed me on the day before my departure that the custom observed at the Institution in all such cases was that the men while in the field paid all their living expenses, except some smaller amounts of an extraordinary nature, which after their return could be refunded. Although I was surprised and disappointed over this severe condition, which, as I told the Director at the time, was contrary to the rules of other similar institutions, I realized that the principal object of mine was now to carry on the investigation and complete my archeological work in Costa Rica, wherefore, I submitting to the rules of the Institution left for the South.

[5] In San Jose, after some legal difficulties regarding the purchase of the Velasco collection had been removed, I could, after a month[']s stay, report to the Director, that I had not only been able to secure the entire collection for a sum of \$2200, but that I had also induced Mr. Velasco to turn over to the Carnegie Museum another collection hardly less valuable, consisting of 2181 specimens, principally ancient ceramics, the only one of its kind from the Pacific Coast, beside my own former, yet undescribed collection, from that region, in Stockholm. This second collection as stated I obtained [end original page 2] without any additional outlay whatsoever of money.

The written instructions mentioned in paragraph 3 refer to Holland's two-page letter of March 24, in which he spelled out the expedition's objectives and charged Hartman with certain responsibilities. Besides buying collections of antiquities, conducting archaeological field research, and working with the Museo Nacional de Costa Rica's collections, Hartman was directed to acquire, as feasible, collections of botanical, entomological, and other specimens for Carnegie Museum. Holland was a respected entomologist and Hartman had been educated as a botanist, so Holland's request for Costa Rican natural history specimens is logical. Paragraph 4 contains Hartman's first reference to the issue of field living expenses, a subject he resurrects later in the letter. Using a clever ploy, he initially raises this issue within the context of his enthusiastic departure on the expedition, despite his disappointment at the severe conditions imposed by the Director's surprising announcement.

Hartman's first mention of the Velasco collection of antiquities in paragraph 3 is followed up, in paragraph 5, by the discussion of his success in acquiring not one but two Velasco collections at a price less than what had been authorized by the Director for the single collection. He used his knowledge of the availability of the first Velasco collection, then "on deposit" at a Philadelphia museum, during his negotiations with Holland, being aware that the Director's priority was to obtain collections for the "infant" Carnegie Museum (Watters, 2002; Watters and Fonseca Zamora, 2002a:282). Although the antiquities were in Philadelphia, Padre José Maria Velasco, the owner who wanted to sell the collection, resided in Costa Rica. Hartman hand-carried to Velasco a letter and draft contract written in Spanish by Holland, and, on April 18, 1903, he sent Holland a cable (Fig. 1) confirming the purchase of the first collection. In a letter written the same day he told Holland of his success in acquiring the second Velasco collection, this one located in Costa Rica. In May, Holland wrote and later visited Mrs. Cornelius (Sara Y.) Stevenson, Secretary of the Board of Trustees, Museum of Science and Art, University of Pennsylvania, to lay claim to the first Velasco collection in that museum's "custody."

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Doctor Holland
Carnegie Museum
Pittsburgh
Velasco collection obtained
Hartman

(Bk OT)

Fig. 1.—Hartman's cablegram of April 18, 1903 announcing the purchase of the first Velasco collection. In a letter written the same day, he told Holland of his success in obtaining a second collection from Padre Velasco. (Hartman Archives, Section of Anthropology).

Hartman went to Philadelphia in March 1904 to inventory, pack, and ship the first Velasco collection to Carnegie Museum, where it joined the second collection which he had sent directly from Costa Rica in 1903. He resumes discussion of the Velasco antiquities later (paragraphs 17 and 18) in the Mellor letter, dealing at length with their scientific value. Velasco had known Hartman since the Swedish expedition, when he denied Hartman's request to join his dig at a site on the Nicoya peninsula (Hartman, 1907:13). The undescribed Pacific Coast collection in Stockholm, noted in paragraph 5, refers to antiquities purchased by Hartman while in the Nicoya region, after failing to obtain Velasco's permission to excavate.

[6] I could also inform the Director, that I had discovered not far from the Capital an extensive burial-ground containing an entirely new class of pottery, representing a highland culture heretofore never described. At that place I obtained during my own excavation more than 1000 specimens of pottery and stone implements. On receipt of this information, the Director in a letter dated Pittsburgh, May 1st, wrote me as follows:

"I was greatly pleased to receive your cablegram, and to have the cablegram confirm your letter of April 8th [sic, 18th], which is before me, and which I had the pleasure of reading to several of the Trustees who are connected with the Committee in charge of the museum. They, as well as I am are [sic] very much gratified with the success which has attended your efforts."



Fig. 2.—Costa Rican field workers employed by Hartman to excavate the Chinchilla site in 1903. (Section of Anthropology glass-plate negative G988).

[7] From that time on I carried on excavations with a number of men [Fig. 2], both on the hoghland [sic] as well as on the Pacific and Atlantic Coasts. I secured what must be considered very valuable authentic material from various burial-grounds and sites of which none ever before had been entered by any archeologist. My old friendly relations to the Director of the Natural [History] Museum of Costa Rica, Professor H. Pittier de Fabr ga, made it possible for me to obtain the enviable privilege to make a thorough study of the undescribed archeological treasures of that institution, and even to secure a collection of hundreds of photographs, a selection I made of the most interesting specimens of said museum.

Paragraphs 6 and 7 briefly discuss Hartman's field research and his study of collections housed at the Museo Nacional de Costa Rica (Watters and Fonseca Zamora, 2002a:fig.8). Hartman's quotation, in paragraph 6, of Holland's comments in the May 1 letter, in response to Hartman's letter of April 18 (not April 8), is a subterfuge. He positions the quotation immediately after his comments about excavating the 1000 specimens, implying that Holland's laudatory comments referred to his fieldwork. In reality, Holland's comments in the May 1 letter refer, without a doubt, to the purchase of the Velasco collections and have nothing to do with Hartman's field research. In fact, Hartman never mentioned fieldwork at all in his April 18 letter. Although Holland's comments did not relate to it, Hartman actually excavated an extensive burial ground in the Highlands, the Chinchilla site (Fig. 3), from which he obtained many artifacts.

In paragraph 7, Hartman refers to the excavations undertaken at the Curridabat and Concepci n sites (Skirboll, 1981, 1984a) in the Highlands and the Las Guacas (= Las Huacas) site in the Nicoya peninsula on the Pacific coast (Fonseca Zamora and Richardson, 1978; Fonseca Zamora and Scaglione, 1978; Hartman, 1907; Heckenberger



Fig. 3.—Hartman's excavation underway at the Chinchilla site, in which are visible the cut-out numerals he placed within the slab-lined graves in order to maintain control of provenience data. (Section of Anthropology glass-plate negative G974).

and Watters, 1993). He obtained already excavated “stone idols” for Carnegie Museum from Las Mercedes (see paragraph 11), but he apparently did not excavate any new sites on the Atlantic coast. Hartman spent considerable time working on antiquities at the Museo Nacional, as instructed by Holland, and he extensively photographed its collections for comparative purposes, with the permission of his long-time friend Henri Pittier de Fabrega (Watters and Fonseca Zamora, 2002a:285–286, 289–290, 2002b). Carnegie Museum of Natural History has more than 700 glass-plate negatives and old prints of Hartman's 1903 fieldwork (Fig. 4), the collections he examined at the Museo Nacional, and artifacts he brought back to Carnegie Museum (Hartman, 1910; Watters and Fonseca Zamora, 2001a, 2002: figures 1, 2, 8, and 10, and images in this article).

[8] Another service which I, during this stay in Costa Rica, was enabled to render for the Carnegie Museum, was the locating of an extensive fossil forest near the Pacific Ocean. From this forest [end page 3] I obtained several cases of specimens. Absolutely nothing has as yet been published regarding the fossil Flora of Central America. During my first expedition [the Swedish expedition] to Central America I searched in vain for more than three years for any vestige of fossil plants. This discovery of mine has of two of the foremost living authorities on paleo-botany been characterized as of high importance, and a third specialist in this branch at another American institution has offered, in case I would divulge the secret of the locality, immediately to send down an expedition in order to carry on investigations on the spot.

Paragraph 8 is the most intriguing and yet perplexing commentary in the entire letter. Hartman clearly regarded his discovery of this fossil forest as an important find, and his assessment of its scientific value is underscored by his own initial university training as a botanist (Watters and Fonseca Zamora, 2002a:261). He further validates the significance



Fig. 4.—A different site excavated in 1903, in which rounded stones line the graves. Hartman (1910:fig. 6) places this “small river-boulders” burial ground near San José but does not identify it by name. The photograph may depict the Curridabat or Concepción site. (Section of Anthropology glass-plate negative G1028).

of this find by referencing the three unnamed paleobotanists. Yet, the “several cases of specimens” reputedly obtained are an enigma because the Paleobotany database at Carnegie Museum of Natural History contains no Costa Rican fossil plant records attributed to Hartman (personal communication, Elizabeth Hill, Collection Manager, November 22, 2002). Hartman in the first sentence links his finding of the fossil forest with his service to Carnegie Museum, but in the next sentence he implies, yet does not specifically state, that the fossil specimens had been donated to the Museum.

[9] Shortly before leaving Costa Rica, in the month of October, I was merely by an accident enabled to buy for the Carnegie Museum the finest and most comprehensive private collection of antiquities of the highland regions ever made. This collection had during some thirty years been in the possession of one of the wealthiest land owners of the country. After his death the heirs, now being financially embarrassed, offered the collection at an exceptionally low figure, a twentieth part of the price before asked. The funds then at my disposition were already exhausted, and it was only through loan from Scandinavian and German friends, and by using part of my salary, that I was enabled to make use of the bargain before anyone else, and could buy the entire collection for the nominal sum of \$450. The collection is now catalogued and numbers 3212 specimens. In this collection are precious and unique specimens, a considerable number of which can be valued from \$20.00 to \$100 apiece. Thirty-four cases were required for shipping the collection. Altogether I secured during my seven months sojourn in Costa Rica for the [end page 4] Carnegie Museum ninety-six cases with collections. These collections, now properly numbered, catalogued and described count 12,250 specimens, of which more than 2000 were secured during my own excavations. The rough estimates, which I previously gave the Director and which were published in the annual reports have proved to be far too conservative. In fact they have been doubled.

The antiquities mentioned in paragraph 9 undoubtedly refer to the Troyo collection at Carnegie Museum. Señor José Ramón Rojas Troyo (Hartman calls him Juan, not José), the wealthy landowner who had assembled an extraordinary collection of antiquities from many areas of Costa Rica, bequeathed these items to the Museo Nacional when he died in 1887 (Kandler, 1987:18). Troyo heavily exploited Agua Caliente, located in his coffee plantation, a site he believed to be Pura-Pura, the purported capital of the ancient province of Huarco (Hartman, 1901:48). His wife Dolores carried on the tradition of employing workers to dig archaeological sites, in this manner accumulating another large collection. The antiquities Hartman acquired at such a low price were purchased from the heirs, either the wife or a son of Sr. Troyo. It was the German consul, Felix Wiss, who alerted Hartman to the pending sale and advanced the money needed to purchase the Troyo collection for Carnegie Museum (Watters and Fonseca Zamora, 2002a:287).

The Agua Caliente site, from which came many of the artifacts in Carnegie Museum's Troyo collection, was studied by archaeologists from the Museo Nacional de Costa Rica, in advance of a housing development project (Valerio Lobo, Solís Alpizar, and Solís del Veccio, 1986; Valerio Lobo, 1989; Vázquez L., 1989). They found evidence of habitation and funerary contexts within this large site, in which the major components correspond chronologically to the late period (A.D. 800–1500). Valerio Lobo, Solís Alpizar, and Solís del Veccio (1986:48) regard Agua Caliente as the settlement of a principal person; evidence for similar structures has not been found at other sites in the region, which implies that Agua Caliente held the top position in the regional hierarchy of sites. Thus, Troyo's belief that Agua Caliente was a significant site indeed has merit, although evidence is not sufficient to link it conclusively to Pura-Pura, known from the Spanish historical records.

In the last part of paragraph 9, Hartman provides Mellor with quantified data on the number of cases of collections shipped back, total specimens acquired (an amount much greater than originally estimated), and the number obtained from his own excavations (about 16% of the total). He was able to satisfy Holland's desire for acquiring antiquities for exhibition (Fig. 5) to a degree even astounding to the Director.

[10] My success in the excavations during this short period, I attribute in the first hand to my own local experience in the field; second, to the valuable friendships previously made both among the foreigners, Scandinavians, Americans and Germans, as well as among the natives in various places. Through their generous help and disinterested assistance I was enabled to obtain permission from the owners of the land to excavate in various localities; and owing to the hospitality and courtesy of various of these gentlemen, my expenses were considerably lowered.

[11] As a rule in Costa Rica excessive charges are made for permission to excavate even in the forest lands. I could quote several examples. I might here mention, that the Costa Rican Government at the time of the Chicago [World's Columbian] Exposition, wishing to carry out some collecting at a famous Indian burial-ground on the highlands, was obliged to pay the owner \$2500 for the permission. The result of these latter excavations, according to the publications of the Museo Nacional were some 500 pieces of crude stone implements and pottery. On the extensive territories owned by the River Platt Co., an English concern, which controls about a sixth part of the Republic, and as well as on those of the [end page 5] United Fruit Co., which owns almost the entire Atlantic Coast of the Republic, all excavations are strictly prohibited. But owing to my previous introductions by one of my countrymen, formerly connected with and interested in these companies, I now again obtained permission to excavate on their lands; and on my visit this time to one of the United Fruit Companies [sic] haciendas I was presented by the owner, Mr. Minor C. Keith with a number of large stone idols, and several unique, highly decorated vases. Through the same introduction I too obtained a considerable rebate from the Costa Rican Railroad Co., when shipping the collections.

Hartman effectively used the contacts he made with Costa Ricans and foreign residents during both expeditions; he acknowledges these individuals in the prefaces of his two monographs (Hartman, 1901:2, 1907:3). The intent of paragraph 10 was to apprise Mellor of the varied ways these persons had been of assistance, which then allowed Hartman to



Fig. 5.—An elaborately decorated “jaguar metate” acquired by Hartman in Costa Rica in 1903 (Accession #2793/2248).

once again bring forth the cost-savings benefit. Paragraph 11 contains concrete examples to reinforce the assertions he made in the prior paragraph and, in the final sentence, he closes with yet another example of having reduced expenses. Hartman explicitly contrasts his success in reducing costs with the heavy expense incurred by the government of Costa Rica to secure an unimpressive collection of artifacts from the “famous Indian burial-ground.” This event refers to the 1891 excavations conducted by Anastasio Alfaro, head of the Museo Nacional de Costa Rica, at the Guayabo de Turrialba site, from which he acquired materials for exhibition at international expositions (Fonseca Zamora, 1992; Murillo Herrera, 2002:23; Watters and Fonseca Zamora, 2002a:268–271).

The commentary about Minor C. Keith allows Hartman to draw together several related elements. Keith, an American entrepreneur who constructed railroads in Costa Rica, developed extensive banana plantations on the Atlantic plain, eventually forming the basis of the United Fruit Company. An avid collector, Keith assembled an extraordinary collection of antiquities from archaeological sites on lands he owned (Mason, 1945; Stewart, 1964:160–168), and he served as a contact for Hartman on the Swedish and Carnegie Museum expeditions. The “large stone idols” presented to Carnegie Museum were from Las Mercedes, a site Hartman (1901:7–39) had dug with Keith’s permission in 1896.

[12] About the intrinsic or commercial value of the Costa Rica collections of the Carnegie Museum, I beg the [Chairman’s] permission to add a few words.

[13] For a fair and just valuation of said collections in comparison with the prices paid by other institutions will undoubtedly form the best basis. In all the American museums there has heretofore only been exhibited two or three rather insignificant collections from Costa Rica, none the result of any scientific expedition.

[14] In Europe there are three large collections, the one in the Stockholm Museum secured by me through excavations carried on for a long period, and two others. Of the latter one belongs to the Imperial Museum of Vienna, and was by the Director, Mr. Hegar, purchased in the year 1896 from the Austrian Consul in San Jose. This collection, which I, myself, had the opportunity of studying in the latter city, contained little more than 1000 specimens, mostly pottery all from the highlands. The price paid was 10,000 Kronen (\$2500). [end page 6] The third Costa Rica[n] collection in Europe is the one of the Museum in Bremen. This one was formed through many years collecting by the then German Consul in San José, and by some wealthy merchants purchased for 10,000 Marks (\$2500) and presented to the institution of their native city. This information is published in "Abh. v. naturw. Vereine zu Bremen, VIII, 1863 [sic], p. 233."

[15] According to the prices thus paid by these well known scientific institutions, the monetary value of the entire collections procured by me for the Carnegie Museum, being by far the most extensive in any institution, would certainly be considered very high, even with due allowance for a large number of fragmentary and minor specimens, which also occur in all other Costa Rican collections. Beside it must be remembered, that the Carnegie Museum collection includes the largest assembled amount in existence of carved and polished objects of the precious mineral jade.

Paragraphs 12 through 15 are Hartman's way of allowing Mellor to compare the Costa Rica collection of Carnegie Museum with those held by other institutions, particularly European museums. Those he chose to include or omit are of special interest. He included only museum collections, thereby ignoring private collections such as Minor C. Keith's enormous holdings (Mason, 1945; Spinden, 1915). In paragraph 13 he glosses over collections in museums in the United States, neglecting to mention, for example, Branford's collection at the United States National Museum, Smithsonian Institution, a collection of which he was perfectly well aware (Hartman, 1907:10–11).

Instead, he focuses on three collections in European museums. Hartman briefly mentions the collection he secured for Stockholm's Royal Museum of Natural History during the Swedish expedition (Brunius, 1984; Watters and Fonseca Zamora, 2002a: 266–267, 279–280), but dwells more on the collections in Vienna, Austria and Bremen, Germany, each of which had a monetary value associated with it. The Bremen collection, the earlier one exported from Costa Rica, was assembled by the German consul, Johann Friedrich Lahmann. Wealthy citizens of Bremen purchased the Lahmann collection and later, in 1879, presented it to the Museum of Natural History (Hartman, 1901:47–48, 1907:9–10). Jones (1998:11) indicates this collection originally was deposited in the *Sammlungen für Naturgeschichte und Ethnographie* and today reposes in the *Übersee-Museum*. Neither of the early articles (Fischer, 1881; Strebel, 1884) published on the Lahmann collection appeared in 1863, as Hartman erroneously stated. The Austrian consul, Guido von Schroeter, obtained Vienna's collection in 1895. Hartman observed the Schroeter collection in Costa Rica in 1896, the same year it was sent to Austria (Hartman, 1901:49, 187–188), and saw it again at the Imperial Museum in Vienna in 1908 (Hartman, 1910). In paragraph 15 Hartman very favorably evaluates the Carnegie Museum collections he had procured, though he waits until a little later in the letter (paragraph 18) to provide a comparative monetary value.

[16] Regarding this matter I refer to the following quotations of eminent American and European authorities reproduced in the annual report of the Director for the year 1905 [Holland's introductory sentence is followed by the quotations from Cushing and Uhle, each of which is preceded by an introductory clause written by Holland]:

It was in reference to one of the latter collections, the Velasco collection, that that eminent authority on American Archaeology and Ethnology, the late Professor Frank Hamilton Cushing made the following statement:

"This collection is of superlative importance to science. In the first place it is intrinsically valuable, consisting as it does of jade, jadeite, fine terra-cotta, shell, and gold. In the second place there is no single collection of aboriginal American art works in stone, in any museum in America, or, so far

as I am informed, abroad, that can compare with this one as to the number of examples it contains of superbly carved, polished, and finished specimens, that are at the same time of the highest artistic beauty even from our standpoint. So true is this that I venture to say [end page 7] that no lapidary would undertake to duplicate the stone series alone for less than four times the price, that is charged for this entire treasury of ancient American gems. But, above all, the collection is unique among American collections of its kind thus far gathered in scientific importance of a very definite sort. It abounds in types illustrating not only the origin of many forms of weapon, symbol, and decoration, but also of the part myth and religious concept play in the modification conventionally, of all these things Were I a man of large means, or of even only moderate means, I would unhesitatingly buy the collection, if only for the sake of having it to study and publish, illustrated, to the world."

Another well known authority in the field of South American archaeology, Professor Max Uhle wrote lately about this same collection:

"As the basis for a representative collection of Central American antiquities I consider the Velasco collection of extraordinary importance. It comes from a province of Central America most important from a historical point of view. It seems to me, with my knowledge of the richest European and other Museums, to be unique in its wonderful implements of stone and according to my modest experience, as far as objects of jade and nephrite are concerned, unequaled by any collection in the world. We shall have to inquire more closely into the relations once existing between the tribes of Central and South America in the near future and it would be difficult to find another collection as appropriate as this on which to base the investigation of the connecting links."

[17] Daniel G. Brinton, professor of American archeology at the University of Pennsylvania gave the following as his opinion[:]

"No other collection equalling this one has been made from Costa Rica. It is well located and very typical of the culture of the natives from whose territory it comes. The abundance in it of jade or nephrite objects is remarkable, and renders it unique and valuable for this alone. Probably no equally fine line of specimens from those tribes will again be offered. Both from the ethnographic and the artistic point of [end page 8] view, it has exceptional merit. The price asked is quite moderate and no one could duplicate such a collection for such a sum."

[18] I am convinced that if a proper valuation should be made by the men, who today are the best authorities on Spanish American archeology, their estimate of the C. R. collections, secured by me for the Carnegie Museum, would reach a sum not less than twenty to twenty-five thousand dollars. Of the sum of \$5,000 appropriated by the Museum Committee for my purchases and fieldwork in Costa Rica only about \$4,700 were actually used in the field.

Paragraph 16, comprising Holland's introductory statement and the lengthy quotations from Cushing and Uhle, is actually cut out from pages 26–27 of the *Annual Report of the Director for 1905* (Holland, 1905) and pasted down in Hartman's letter to Mellor. Thus in paragraph 16, Hartman is quoting Holland who in turn has quoted Frank Hamilton Cushing and Max Uhle, two prominent archeologists of the time. The passage by the eminent anthropologist Daniel Brinton, quoted in paragraph 17, does not appear in that *Annual Report*. Holland does not identify the sources of the Cushing and Uhle quotations, nor does Hartman identify the source of the Brinton quotation he inserted in the Mellor letter.

Three letters examined in the University of Pennsylvania Museum Archives (American Section—Velasco Collection, 1898), addressed to Stewart Culin, then Director of the Museum of Science and Art in Philadelphia, bear on the issue of sources. The letters from Cushing and Brinton, dated February 18, 1898, and Uhle, dated February 21, rue the possible loss of the Velasco collection of Costa Rican antiquities held at that museum. They exhort Culin to purchase the collection before another institution can do so and laud its aesthetic and scholarly importance. Culin orchestrated the production of these letters. A few days before, on February 15, he had received a letter from William P. Wilson, Director

of the Philadelphia Museums, indicating that the owners of the collection wanted it sent to the Costa Rican consul in New York City for onward shipment to England, although Wilson informed Culin he “. . . could still purchase it in all probability if you desire to do so.” Cushing, Brinton, and Uhle wrote their letters to support Culin’s efforts to raise money to purchase the Velasco collection. One other document held in the University of Pennsylvania Museum Archives directly connects these letters with Carnegie Museum. A hand-written note, dated May 16, 1903, discloses that copies of the Wilson, Brinton, Cushing, and Uhle letters were “. . . handed to Dr. Holland at Mrs. Stevenson’s order.” Holland’s rendering in the *Annual Report* of Cushing’s comments is a verbatim quotation, except for minor editing, of parts of Cushing’s February 18, 1898 letter. Holland created Uhle’s quotation in the *Annual Report* by drawing together parts extracted from Uhle’s February 21 letter. Hartman was more faithful to Brinton’s original passage, extracting and presenting verbatim the body of the text in the February 18 letter, omitting only Brinton’s introductory sentences and ending sentence that dealt with the situation in Philadelphia in 1898. Thus, in the *Annual Report*, Holland quoted two reputable persons regarding the value of Velasco’s collection (and by extension all of Hartman’s Costa Rican collections), but he somewhat deceptively drew upon letters they wrote five years before Carnegie Museum acquired the collection (seven years before the 1905 *Annual Report*), when it was buyers in England, not Pittsburgh, who posed a threat to Philadelphia’s retention of the antiquities. Hartman deftly followed Holland’s strategy by inserting Brinton’s quotation, by then nine years old, into the 1907 letter to Mellor as further support for the value of the Velasco collection and, by extension, for his request for a raise.

In paragraph 18, Hartman estimates the monetary valuation of Carnegie Museum’s Costa Rica collections. He implies that the best authorities on Spanish American archaeology, whom he does not name (though Mellor had just read of Cushing, Uhle, and Brinton in the immediately preceding paragraph), would place a monetary value of \$20,000 to \$25,000. A careful reading of this paragraph shows that the estimate given really is Hartman’s “conviction” of the value of the collections, and is not a valuation that was provided by the unnamed authorities. In the final sentence, just after having given the substantial valuation, Hartman brings forth once again, almost parenthetically, the “reduced expenses” argument concerning his fieldwork.

[19] Other collectors, but with less practical training, have tried the Costa Rican field but with little success. During the preparations for the World’s Fair [Columbian Exposition] in Chicago a collector was dispatched by Professor Putnam and provided with means for securing archeological material from Costa Rica. He spent several months in the country but was only able to pick up a few specimens here and there, altogether two or three small boxes. Last year I was approached by Mr. George Heye of New York, who yearly spends more money than any public museum on this continent for purchases and excavations in order to obtain archeological material. He asked me as a favor, that I would give information and advice to one of his special collectors, who formerly had worked in Porto [sic] Rico. He wanted to send him down to Costa Rica for some months and was willing to place very liberal funds to his disposition. I gave this gentleman all the information I possibly could about localities, methods of work[,] and provided him with letters of introduction to my best friends in Costa Rica. I was much interested [end page 9] in his success, as Mr. Heye generously offered to place all the collections he could secure to my disposition for publication. However, his sojourn in Costa Rica was practically a failure. I was shown the results, which consisted of possibly some 50 small specimens of pottery picked up in the houses of the natives.

[20] For a comparison when judging of the value of similar collections, I will here mention the price lately paid for a collection of South American pottery by the curator of anthropology at the Field Museum, Dr. [George] Dorsey. At the St. Louis Exhibition [Louisiana Purchase Exposition] he gave \$16,000 for a collection consisting of 4500 pieces of archeological specimens from Argentine [sic], obtained by a native collector.

In paragraph 19, Hartman contrasts his achievements, presented in the preceding paragraphs, with the largely fruitless efforts of others working in Costa Rica. Watters and

Fonseca Zamora (2002a:270) discuss the historical context of Frederic Ward Putnam's unsuccessful attempt to obtain antiquities in Costa Rica for the World's Columbian Exposition. George Heye, a wealthy collector of antiquities and founder of the Museum of the American Indian, Heye Foundation in New York City, routinely sent persons to areas of the western hemisphere to purchase ethnographic and archaeological materials on his behalf. The unnamed special collector's practical failure, even after having received valuable information from Hartman and being well funded by Heye, stands in sharp contrast to Hartman's accomplishments for Carnegie Museum, a diametrical opposition of results that, even though unstated, he knew would be self-evident to Mellor.

Why Hartman included paragraph 20 remains uncertain. Its intent may have been simply to provide an example of a supposedly comparable collection's high cost. Or it may have had a more subtle intent, perhaps pointing out the liberal funds being made available to his counterpart curator by Field Museum.

[21] The most telling proof of the really high value of the material I secured is the fact, that the greatest portion of the duplicates at least 8,000 specimens can easily be disposed of for exchanges. I have already from the American Museum of Natural History, and from the Yale University Museum obtained fine collections of material from Chiriqui in Columbia [sic], from Mexico, from the West Indian Islands, from Guatemala and Peru, and I have offers from the museums in Washington, Philadelphia[,] Cambridge[,] and San Francisco to obtain additional archeological material from many other parts of Spanish America. In this way, without any extra expense, a very considerable space in the exhibition halls will be filled with first class material. At present we have a selection of little more than two thousand specimens of Costa Rican ware on exhibition. Most of the rest is available for the purpose mentioned. A number of the unique stone sculptures of Costa Rica are now reproduced by Mr. Mills, [end page 10] and for this material we will also be able to obtain casts from various sources.

[22] All the other collections in my section, with few exceptions, are on the other hand already previously represented in other American museums, and the duplicates from these collections are of comparatively little value for exchange purposes.

Paragraph 21 highlights the potential of the Costa Rican materials, regarded as duplicates, for exchange with other museums. Exchanges with the Yale University Museum (CMNH Acc. #4290), now Peabody Museum of Natural History, Yale University, and the American Museum of Natural History (CMNH Acc. #4291), arranged respectively with George Grant MacCurdy and Clark Wissler, were completed during Hartman's tenure at Carnegie Museum (although they were not accessioned until 1911). The Chiriqui antiquities exchanged by MacCurdy (1911) came from a region (in present-day Panama) still belonging to Colombia when the collection was made. The West Indian artifacts exchanged by AMNH are from Guadeloupe, Puerto Rico, and Barbados (Watters and Brown, 2001). The purported offers made by museums in Washington, Philadelphia, Cambridge, and San Francisco apparently never were realized since no records of such exchanges have been found. The estimate of slightly more than 2000 Costa Rican artifacts being on exhibit refers to the new Gallery of Archaeology opened in April 1907 in the expanded Carnegie Institute facility (Watters and Fonseca Zamora, 2002a:282). Paragraph 22 reinforces Hartman's arguments for the importance of the materials for exchange purposes, thereby providing Carnegie Museum with a "bargaining chip" to obtain artifacts from elsewhere in the world, from those museums desirous of acquiring Costa Rican objects.

[23] Of much higher importance than the gain made through the addition of these collections must be considered the scientific results of the work in the field embodied in the observations, plans and photos obtained and of which a portion is now issuing from the press.

[24] That my former work in Costa Rica has won the approval of the foremost authorities in American Archeology is known to the Committee through documents I submitted four years ago containing [the] opinions of Professor Eduard Seler of Berlin, Dr. Franz Boas of Columbia University, Dr. W J McGee and Professor A. B. Meyer of Dresden.

[25] Since that time various reviews and comments upon my publication "Archaeological Researches in Costa Rica" have appeared in the scientific press. A few are here reproduced.

[26] At the 13th International Congress of Americanists assembled in New York a resolution was proposed by Professor F. W. Putnam, in his capacity as one of the presidents of the Congress, seconded by Professor Franz Boas and unanimously adopted by the Congress. From that resolution the following is an extract: [end page 11]

"Resolved, that the members of the 13th International Congress of Americanists, assembled in New York, hereby express their hearty appreciation of the results attained by the Archaeological Expedition to Costa Rica under the direction of Mr. C. V. Hartman and they congratulate Mr. Sjögren upon the magnificent manner in which the Report has been published." [The work is further characterised, later on, as:] "the most painstaking and elaborate Report of the exploration of ancient graves in Central America which has ever been undertaken," [to which is added the further remark:] "the beautiful volume will always serve as a model for this class of archaeological work." [For clarity, we bracketed two phrases inserted by Hartman in the Mellor letter, which were not contained in the text of the original resolution.]

[27] In the "Journal of the Anthropological Institute of Great Britain and Ireland," an extensive review of the work is given by the Secretary of the American Anthropological Association, Dr. George Grant MacCurdy. From this a couple of paragraphs are here reproduced:

"Museum collections and special publications derive their value from the character of the field-work on which they are based. Nowhere, not even in the studio, does skill, training, the touch of the master, count for more. Measured by such a standard, Mr. Hartman's publication cannot fail to be classed as one of exceptional value. It is with such material as he has furnished that we may some day hope to raise American archaeology to the dignity of a real science. . . . Ever since the time of Thomsen and of Worsaae, the world has been accustomed to look to Scandinavia for light and leading in the realm of prehistoric archaeology. To Mr. Hartman belongs the credit of transplanting to [end page 12] American soil the seeds which have borne such excellent harvests in Denmark, Norway and Sweden. May he have abundant opportunity to do field-work of the same high grade for the Carnegie Museum as that which he did, through the munificence of Mr. Sjögren, for the Swedish Museum.["]

[28] At the International Congress of Arts and Science at St. Louis [held at the Louisiana Purchase Exposition] the scientist, who was invited as the official speaker on Archeology, Professor Eduard Seler in his address on "The Problems of Archeology" (Vol.V. p. 535) made the following reference to my previous work:

"The region comprising Mexico and Central America is that in which American archeology is best able to rise above the standpoint of merely antiquarian investigation and to attempt higher tasks. . . .

A limited region, including the old settlements on the slopes of the volcano of Irazu and certain groups of hills which extend down into the Atlantic lowlands, has lately been investigated in a really exemplary manner by C. V. Hartman, whose results have been published in a sumptuous work, distinguished by the Swedish Academy with the Duke of Loubat[']s prize. Outside of this, to be sure, we still (in Central America) lack excavations undertaken in a scientific manner and authenticated by documents.["] [Seler's (1906:536) original text misidentifies him as E. V. Hartman and does not include (in Central America), a parenthetical phrase inserted by Hartman in the Mellor letter (Watters and Fonseca Zamora, 2002a:271)].

[29] When in 1902 the Scandinavian Loubat prize was awarded to me (with 17 votes of 19) I had as competitors the then President of the Swedish Anthropological Society, Dr. F. Dahlgran and the author of the 'Origin of Art,' Professor Yrjö Hirn of [end page 13] the University of Helsingfors. The prize is distributed every fifth year. This year [seemingly referring to 1907] however the Academy decided that no prize could be awarded to the three applicants, Dr. Carl Lumholtz of Krisitanian, Dr. Stenneyby of the Copenhagen National Museum and Baron E. Nordenskiöld, assistant Director of the Ethnographical Museum in Stockholm.

Paragraphs 23 through 29, dealing with the scientific significance of Hartman's archaeological research, were included to bolster his case for the high quality of his scholarship. Hartman's (1907) monograph in the Carnegie Museum *Memoirs* series was "issuing from the press" about two months after he wrote Mellor. His comments, therefore, address the acclaim he received from colleagues for his earlier research, for the Royal Museum of Natural History of Sweden, and the praise accorded his first monograph, *Archaeological*

Researches in Costa Rica (Hartman, 1901). Eduard Seler, Franz Boas, W J McGee (he omitted periods after his initials), and A. B. Meyer were respected anthropologists whose “excellent testimonials” Hartman provided to Holland while seeking employment at Carnegie Museum (Watters and Fonseca Zamora, 2002a:281–282, 2002b). The extracts (in paragraph 26) from Putnam’s highly complimentary resolution at the International Congress of Americanists are the only surviving passages of the original resolution, which was not published in the proceedings volume (Watters, 2002; Watters and Fonseca Zamora, 2002a: 274–275). The quotations Hartman selected from MacCurdy’s (1905) review of his 1901 scholarly monograph and from Seler’s (1906) remarks about his research in Central America were well-suited to buttressing his professional reputation. The Duc de Loubat prize, conferred upon him by the Royal Academy of Belles Lettres, History, and Antiquities of Sweden, was a prestigious award of which he rightfully was proud (Stolpe, 1905). In these paragraphs, he indeed does make a strong case to Mellor about his professionalism and scholarship.

[30] The above statistics regarding the visible results of my work as a collector and the quotations regarding the quality of scientific work previously accomplished furnish some guarantee, that I even in the future might be able to do the Carnegie Museum valuable services particularly in Mexico and Central America, the regions which according to the wise plans of the Director were from the very beginning selected as the special field for the prehistoric researches of the Carnegie Museum.

[31] The same field will probably soon be entered by the Carnegie Institution of Washington, if the appeal now made to the same by all the anthropological societies of America for the creation of an anthropological department is favorably acted upon. This application, which I recently had the honor to sign, calls for an annual appropriation of \$40,000 to be used exclusively for prehistoric anthropological researches in Spanish America and in this the urgent importance of more work in Central America the cause-way for the races of the [sic] both continents is dwelt upon.

[32] If properly continued and extended the work already inaugurated on a small scale by the Carnegie Museum will surely become a valuable link in the chain of investigations projected to be [end page 14] carried out by the sister institution of Washington and will in the future aid in solving the problems of the first appearance and development of the American race.

[33] During my previous seven years of explorations in Mexico and Central America, I have obtained the most definite information about the best localities both for ethnological and archeological work. From some of my personal friends, Swedish Americans, who control an extensive tract of land, covering many square miles near the Guatemalan frontier, I have recently got [an] invitation to explore extensive ruins and burial-grounds for the Carnegie Museum, being assured of all possible assistance. They have even offered me free passage.

Paragraphs 30 to 33 are future-oriented and hold out the promise of great things that could be done by Carnegie Museum, with Hartman’s implicit participation. He follows up on his “old plan” (paragraph 2) for broader research in Spanish America, the “special field” also wisely selected by the Director, and makes mention of his own work earlier in Mexico and Central America (Watters and Fonseca Zamora, 2002a:264–267). In paragraph 33, he returns to the theme of the advantages accruing from his personal contacts, with the possibility of a new project at “reduced costs” (free passage) in Guatemala. His reference to Carnegie Institution of Washington in paragraphs 31 and 32 can be interpreted in two ways. On the one hand it may be an allusion to the promise of collaboration between the sister institutions. However, the comments also might be interpreted as implying, or at least suggesting that the new institution held greater promise for fulfilling Hartman’s research agenda.

[34] Shortly before I left Europe, I devoted some time to become instructed by specialists in two new, advanced technical methods for certain lines of anthropological research, methods which have proved highly time and labor saving and through which far more accurate results can be attained than at present is possible. None of these methods has as yet been put in practice in America. I should be glad to make use of the same as soon as possible in my work for the Carnegie Museum, being absolutely convinced that these methods once introduced in the Western Hemisphere will supersede the older and become adopted by all other workers in the same field.



Fig. 6.—Hartman photographed the numerical designators he placed in Chinchilla graves, before, during, and after excavation. (Section of Anthropology old print OP13; “old print” refers to an image printed when Hartman was at Carnegie Museum, for which the corresponding glass-plate negative cannot be located today).

Paragraph 34 not only emphasizes Hartman’s capability as a field worker but also reiterates, for Mellor’s sake, his aptitude for applying new field methods (Fig. 6). Hartman first touted his knowledge of new archeological field methods in his letters of January 28 and February 20, 1903 to Holland, while negotiating for a position at Carnegie Museum

(Watters and Fonseca Zamora, 2001*b*). He makes the same points to Mellor, emphasizing the techniques' superior accuracy and their savings in time and labor. He first used them in Costa Rica during seventeen months (May 1896–September 1897) of fieldwork on the Swedish expedition, when he faithfully employed the methods he had learned the year before in Sweden from his mentor Hjalmar Stolpe (Lindberg, 1996; Watters and Fonseca Zamora, 2002*a*:279, 2002*b*). His proficiency in applying these techniques, in the systematic excavation, meticulous recording, and photographic documentation of the burial contexts at cemetery sites is evident in his monographs (Hartman, 1901, 1907). His high standards of fieldwork truly were unusual for the time, a point resurrected many years later by Rowe (1959) and subsequently endorsed by Baudez (1967), Fonseca Zamora (1984, 1992), Skirboll (1984*b*), Ohlsson de Formoso (1991), Willey and Sabloff (1993:85), and Jones (1998).

[35] Opportunities for the development of the Section under my care on the lines contemplated are consequently bright enough.

[36] I wish, however, to emphasize the fact, that I hope the Museum Committee will now since Mr. Carnegie has provided the [end page 15] institution with an endowment larger than that of most of the leading museums of the world encourage my efforts by an increase of my salary [\$2000 per year since 1903], paying me in the same way as other American institutions do. The average salary of curators at other institutions is \$3000 and several curators receive \$3500, and have at the same time liberty to devote perhaps the greatest part of their time to other duties as teachers, in this way almost doubling the salary mentioned. At the Field Museum the assistant curators in the anthropological department are each paid \$2500 per year. The assistant Curator of Ethnology at the American Museum in New York has since years ago been paid at least \$2200, but is free to use about half of his time for the preparation of lectures and for teaching at other institutions from which he also draws salary.

[37] I was distinctly told by the Director, at the time the agreement was made, that I would have to work under the same rules and regulations and with the same salary as the other curators of the museum. I was also told, "that when after a couple of years the Institution had been opened and endowed, I could gather my assistants around me just as Mr. Hatcher did, that a fine anthropological library would be provided my Section and that in every way encouragement should be given."

[38] I realize of course that the delays of opening the Institute have made it difficult as yet to realize all these prospects. I have still here in Pittsburgh[h] to work under the very great [end page 16] drawback of practically being without any library for study, identification of specimens and references, etc. Books have been bought from some hundred dollars, but even a sum of \$10,000 would not go very far to lay the foundation for an anthropological library. At least one assistant with any scientific training is another of the very essential needs of the section.

[39] However, the comparatively small matter of satisfying the requests for an increase of the curators' salaries, I presume can already now be settled so much the easier as the museum counts only two curators on the staff.

The single sentence in paragraph 35 is the transition between the laudatory comments earlier in the letter and the concerns that were foremost in Hartman's mind, those being the issues revolving around his remuneration at Carnegie Museum. He carries forward the transition in paragraph 36 by making reference to the endowment provided by Andrew Carnegie, cleverly linking it to a salary increase that would further encourage his efforts, and then providing data on the higher salaries paid for similar positions at comparable museums. In the next two paragraphs he initially acknowledges the conditions imposed by Holland at the time of hiring, then alludes to certain assurances of future support that had been made by the Director (presented as if quoting him), and finally lists some of the constraints (especially an inadequate anthropological library) under which he was working, implying that the purported "promises" were unfulfilled. In paragraph 37, Hartman cleverly refers to the assistants who had been authorized for Mr. Hatcher (John Bell Hatcher, Curator, Section of Paleontology, who had died in 1904), and then deftly ends paragraph 38 by pointing out the parallel need in his Section for at least one scientifically trained assistant. Paragraph 39 is a *tour de force*, as Hartman revisits the issue

of salary increases, but adroitly alludes to the situation being a small matter that can be readily settled since the Museum then had only two curators. In doing so, he manages by inference to refer indirectly to the concurrent letter being submitted by Ortmann to Mellor.

[40] I have a special reason to consider, that I might be remembered now and that is the fact, that although I was informed that the results of my work were gratifying I still had to pay my living expenses while in the field. As said before this is contrary to the rules of all other large institutions in America. At all the other museums as in New York, Washington, Chicago, San Francisco and Philadelphia, the men while on expeditions for months or years have their expenses paid on a liberal basis.

[41] In the printed regulations of one of the great Washington institutions I find stated "that all employees while in the field for studies or collecting have their living expenses paid, and this includes the expenses at hotels, the price of \$5.00 per day not to be exceeded. All such comforts and minor items as laundry, bath, sleeping cars, tips for porters and waiters, streetcar fares, etc., are also provided for." [end page 17]

[42] From a scientist, who certainly has practical experience in field-work of every description just in Central America, a man who has lived and traveled there for about twenty years, the former Director of the Museum of San Jose, Professor H. Pittier, now since some four years ago engaged by the Government of the United States for botanical collecting and investigations in all parts of Mexico, Central and South America, I recently had a letter with the statement that he in Central America considers as moderate his own average living expenses of about \$150 per month.

[43] In Frank Carpenter's reliable work on South America the average expense of a white man is given as \$10, per day and I am informed, that the scientific collectors of the Commercial Museum in Philadelphia, were allowed \$15 per day for living expenses in Spanish America. In fact I know myself that \$7 to \$12 per day is considered the average expense of the commercial travellers in Central America.

[44] The fact that I was able to save anything at all out of my salary while in Costa Rica depended exclusively on the great hospitality of my old friends down there and upon my adoption of the very primitive way of living of the natives, conditions often such that those of any Hungarian or Italian laborer's [sic] camp in the United States, in comparison must be considered luxurious.

[45] What I saved was after my return to Pittsburgh very soon swallowed up by the outlays for several new suits, instead of those I had spoiled entirely during the rough life in the wilderness, and by doctor's bills on account of my anemic condition, caused by [end page 18] several months['] work in malarial regions during the rainy season, and last but not least by a considerably increased life insurance, also caused by impaired health.

[46] I remember well, that I after my return was allowed a certain moderate sum, but this one was smaller than the sum of \$135, which I had paid out of my own pocket for the three copies of my book which I presented to Messrs Keith, Pittier and Ferraz as an appreciation of their services on behalf of my expedition.

In paragraph 40 Hartman returns to the issue of field living expenses, a point he first raised in paragraph 4. Documents in the Hartman and Holland Archives leave no doubt that this issue was a galling matter for both individuals. Hartman failed to provide the Director with a monthly accounting of his expenses, as was required in the two-page letter of instruction he received before departing for Costa Rica. When he finally did submit an expense report, after being there about three months, he included costs that were unwarranted in Holland's view. After Hartman's return, they met to review his accounting for "extraordinary" living expenses, and Holland disallowed the reimbursement of a number of items for which Hartman felt he was entitled, as he notes in paragraph 45 with respect to two suits he ruined during the fieldwork (Fig. 7).

In paragraphs 41 through 43, Hartman compiles an impressive array of facts from various sources to back his argument for warranted field expenses and, at the same time, to show that Carnegie Museum was unique in not providing for those costs. He reiterates in paragraph 44 the cost-savings resulting from his friends' hospitality in Costa Rica, first noted in paragraph 10, and mentions the money he saved by adopting a primitive way of living (cf. Molina Jiménez, 1991). Paragraphs 45 and 46 continue the litany of costs that he had incurred in the service of Carnegie Museum, including later expenses in Pittsburgh. Paragraph 45 is significant as well because of his reference to impaired health, seemingly

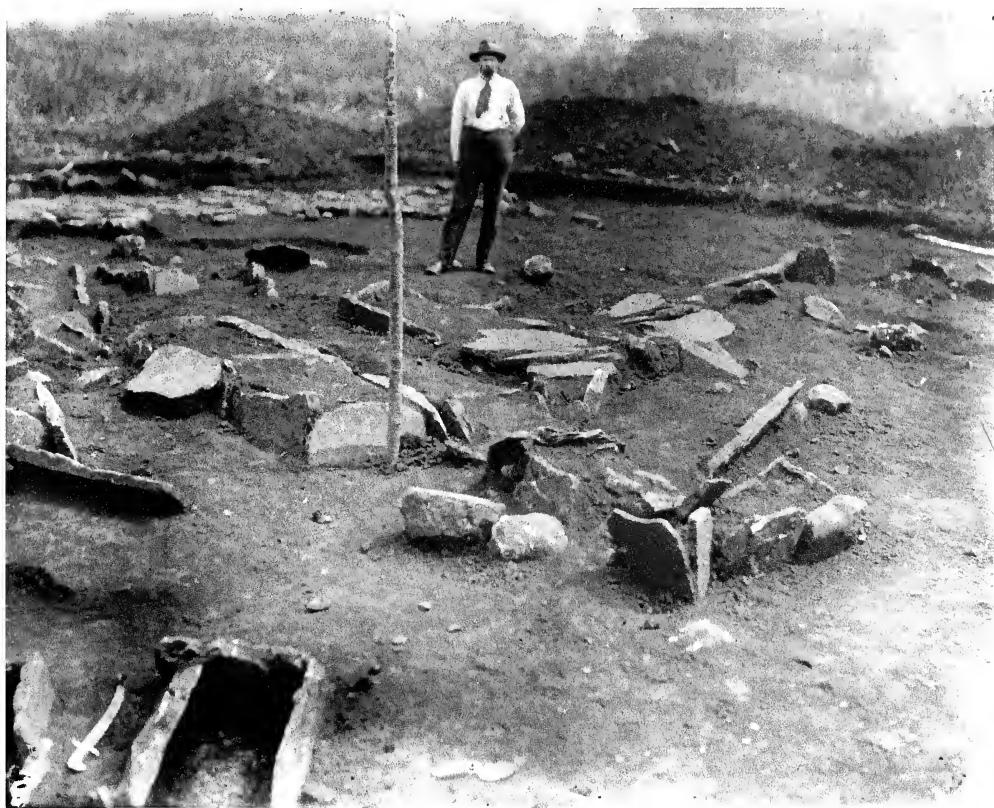


Fig. 7.—Hartman sporting appropriate field attire for a project director in 1903. (Section of Anthropology glass-plate negative G968).

being attributed to malaria, and we know he was ill and often missed work at Carnegie Museum and later he was granted a medical leave of absence from the Swedish Royal Museum of Natural History (Lindblom, 1941; Brunius, 1984; Watters and Fonseca Zamora, 2002a:276).

[47] During the present year no large funds are needed for my section. No rent is longer to be paid for storage etc. No new collections can very well be purchased as all available space in the exhibition cases is already occupied and the two store rooms are nearly filled with boxes with various material. The services of the sculptor, Mr. Mills can from the end of this month again be transferred to the paleontological or transportation departments, as he now has finished the restoring of all the Egyptian and Columbian [sic] ware upon which he has been engaged lately and as there seems to be no place available for more Indian groups.

Paragraph 47 resurrects the “reduced expenditures” theme, this time regarding the Section of Ethnology and Archaeology. The comment about rent no longer be paid refers to the “Annex facility,” a private residence rented by Holland between November 1903 and January 1907 to house Carnegie Museum’s burgeoning anthropological and natural history collections, until exhibition and storage space became available in the expanded Institute building. Hartman had the unenviable duty of being in charge of the Annex facility in addition to his own Section. Hartman’s creative ways of further holding down costs, put forth in the final two sentences, by buying no more collections and transferring the services of the sculptor Theodore A. Mills, are rather ingenious proposals.

[48] I will finally state, that I little more than a year ago was approached by another institution and assured better financial conditions than my present, but as I at that time still had absolute faith in an early realization of the hopes here held out, and naturally was reluctant to interrupt the work, which I had started and was much devoted to, I then declined the offer.

[49] I would appreciate as a special favor if the matter could be definitely settled at this month[']s meeting. [end page 19]

[50] Repeating my sincere regrets over the many details with which I have intruded upon your most valuable time and respectfully asking for your kind and generous support in the matter, I hope that this my first appeal to the Museum Committee will be favorably considered.

I am,

Yours very obedient,

C. V. Hartman [signature]

In paragraph 48, Hartman informs Mellor that he has considered but declined an offer from another institution, noting specifically its better financial remuneration, but he then deftly closes by reasserting his fealty to Carnegie Museum and devotion to his work. In the final paragraphs, he requests a definite resolution of the matter, though without actually mentioning a salary increase, and ends with a respectful appeal for Mellor's support and the Committee's favorable consideration.

Hartman presented Mellor and the Museum Committee with a well-organized letter that contained thoughtfully constructed arguments supporting his appeal for consideration of a raise in salary. He respectfully introduces the salary issue in paragraph 1, reiterates the request only in paragraph 36, and asks for a prompt resolution only in paragraph 49. He deals primarily with his past accomplishments until paragraph 30, where he reorients the text to focus on opportunities in the future, after which he makes the transition (paragraph 35) to his litany of "concerns" about the Director's practices and policies, and then cleverly closes with an indication of his loyalty to Carnegie Museum. The clear implication, though not so stated in the letter, is that the Director, rather than Carnegie Museum, was the root of the "problems" or "issues" Hartman confronted during his period of service.

Hartman well understood the Museum Committee audience to whom his letter was addressed. He spends little time (paragraphs 6 and 7) discussing his fieldwork on the expedition but covers the collections he obtained in considerable depth, culminating in his estimate (18) of their monetary value. He is particularly adept at presenting the Velasco collections, first in terms of his ability to obtain not one but two collections (3 and 5) and later by validating them with the opinions of experts (16–18), even using the quotations chosen by Holland to his advantage, yet he also mentions the Troyo antiquities (9) and even the fossil forest specimens (8). He compares the collections he acquired with those in Europe (12–15), points out their value for exchange with other museums (21–22), puts their scientific results at an even higher level of importance (23–29), manages to slip in a comparison to the paltry results achieved by other collectors (19), and informs Mellor that 2000 of the specimens are newly exhibited (21).

Hartman also incorporated comments about "cost reductions," though they usually were inserted amidst other text. He paid less than the Director authorized for one Velasco collection but got two collections (paragraphs 3 and 5), bought the Troyo collection at an exceptionally low figure (9), spent less than appropriated for his fieldwork (18), and used his personal contacts to reduce his living expenses (10), waive fees for excavating on private lands (11), and get a rebate for rail shipment (11). He saved money by adopting the

“primitive ways of the natives,” though he carried the comparison a bit far when referring to living conditions in laborers’ camps in America as being “luxurious” (44). He even projects reduced costs for his Section (47) and holds out the promise that his acquaintances would hold down future field costs by offering free passage on a new project (33). This litany of savings is a clever strategy because it allowed him to document his fiscal responsibility. The lowered costs he obtained for Carnegie Museum contrast markedly with the personal costs he incurred, such as his two spoiled suits (45) and three books he bought for colleagues (46), which were among the extraordinary field expenses disallowed by Holland, to Hartman’s extreme displeasure (4) and contrary to the rules of other comparable institutions (40–44).

THE SIGNIFICANCE OF THE LETTER

Hartman’s masterfully crafted letter came to naught. He received no raise, continuing to earn \$166.66 per month, the same as his 1903 salary, and less than a year later, on May 1, 1908, resigned as Curator of Ethnology and Archaeology, returning to Sweden to become Director of the Ethnographical Department (also termed the Ethnographical Museum) of the Royal Museum of Natural History (Brunius, 1984; Lindblom, 1941; Watters and Fonseca Zamora, 2002a:280). Hartman’s letter to Mellor is significant for detailing his accomplishments and, it would appear, for the role it played in bringing to a close Hartman’s curatorship at Carnegie Museum.

The Hartman Archives and Holland Archives contain documents speaking to the circumstances surrounding the decision to disallow Hartman’s request for an increase in his salary. The documents also attest to the strained relationship between Hartman and Holland, the issue of Hartman’s impaired health, and the broader concern of inadequate staff salaries at Carnegie Museum. This information appears in four sets of documents: (1) Minutes of the Museum Committee’s meetings between April 30 and September 28, 1907; (2) Monthly Reports of the Director to the Museum Committee between March 31 and October 31, 1907; (3) selected Monthly Reports of the Section of Ethnology and Archaeology, submitted to the Director by Hartman between July 1907 and January 1908; and (4) two letters from Hartman to Holland.

The dedication of the expanded Carnegie Institute facility in early April 1907 was the culmination of Holland’s vision for a new Carnegie Museum, an endeavor to which he had devoted a great deal of effort since becoming its Director full-time in 1901. The rationale presented to the staff for holding salaries steady in the years leading up to the dedication had been the great expense incurred in creating the Museum, from acquiring its collections to installing its exhibit galleries. With the opening of the facility, that rationale no longer held true, particularly when it became known that Andrew Carnegie had provided an endowment to maintain the Museum. The staff wasted no time in lobbying Holland to address the dual issues of postponed compensation and delayed advancement in positions.

The staff approached Holland even before the new building was dedicated, as he informed the Museum Committee:

Rather insistent efforts are being made latterly on the part of several members of the staff requesting advancement in the matter of titles. Some of them think that the positions which they hold are not sufficiently dignified by the titles that have been accorded to them and wish to be advanced in title, and, in several cases, to receive corresponding advances in compensation. These matters I would like to submit to you [the Museum Committee members] and discuss candidly. In one or two cases I think perhaps some concession ought to be made; in other cases I am not at all clear that the demands are justly made in view of the services rendered. (Holland Archives, Report of the Director to the Museum Committee, March 31, 1907).

At the next meeting, Holland devoted one and one-half pages of his report to informing the Museum Committee members about these matters, informing them of the dire consequences that might follow if no resolution was reached:

Many of those who are in the employ of the Museum have been encouraged to remain with us, though offered higher salaries elsewhere, in the hope and belief that at this time, through the kindness of the generous Founder of the Institution, it would be possible to add somewhat to their salaries. These salaries, I may say are much lower than what are paid for similar services in any other institution of like grade in the United States. I am now confronted by the fact that unless relief in some way is provided, I shall not only be forced to disappoint those who have been working on insufficient salaries and who have been led to hope that in return for faithfulness to us their salaries might be increased, but shall be compelled to dispense with the services of many who are now employed in the Museum. (Holland Archives, Report of the Director to the Museum Committee, April 30, 1907).

He then lists several staff members whose departures would be felt severely, and ends by implying that it may be necessary to shut the Museum for the coming year if a resolution is not forthcoming. The Museum Committee took action that very day, approving the Director's recommendations for salary increases for four staff, including a raise for A. E. Ortmann from \$166.66 to \$183.33 per month (Holland Archives, Minutes, Museum Committee Meeting, April 30, 1907). Ortmann's raise took effect June 1. Hartman is mentioned neither in Holland's report nor in the Minutes.

The Minutes of the next meeting record the Committee's receipt of Hartman's letter of May 27:

Chairman Mellor presented two letters received respectively from Mr. Hartman and Mr. Ortmann, of the Museum staff, discussing the question of salaries, expense allowances, etc., which on motion were referred to the Director for such attention as they may require. (Holland Archives, Minutes, Museum Committee Meeting, May 31, 1907).

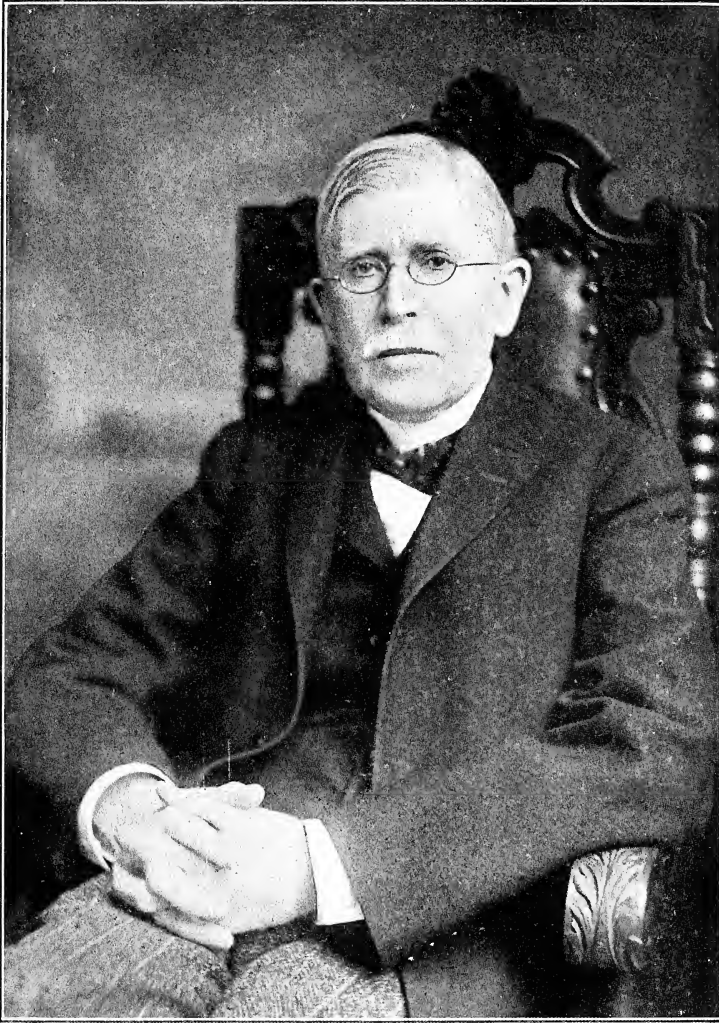
This brief passage is puzzling. Ortmann's salary increase already had been approved at the April meeting of the Museum Committee, so it is unclear why he chose to write the letter received at its May meeting, unless "expense allowances" remained an issue for him. However, Hartman's reason for composing his lengthy letter, submitted just four days before the May meeting date, is logical because by then he probably already was aware that no raise had been granted him at the April meeting. It also would explain his decision to send the letter to Mellor directly, thereby bypassing Holland who had not advocated an increase in his compensation in April. That the Museum Committee referred his letter to Holland for action boded ill for Hartman, especially since the Director and Mellor (Fig. 8), who had been its Chairman since 1896, had collaborated closely on developing Carnegie Museum and had been good friends for many years (Holland, 1909).

Holland made no mention of the issue of Hartman's salary in his Monthly Report of May 31. However, he does refer to him with respect to another matter, in a manner providing insight into his thoughts about Hartman:

Mr. C. V. Hartman has requested me to grant him a vacation in order that he may go to Sweden to attend to some affairs of a personal nature arising, as he states to me, through the recent decease of a relative. He informs me that he has had no vacation since he has come into our employment and intimates that would expect that his salary would continue during his absence. I am willing to concede that he has not been formally absent on a vacation at any time since his coming to us, though he has been away from the Museum a great deal of his time, during which, while he may have accomplished work of importance for the institution, the evidence of its accomplishment is not very apparent to the Director. I would like the advice of the Committee in reference to the matter. (Holland Archives, Monthly Report of the Director to the Museum Committee, May 31, 1907).

ANNALS CARNEGIE MUSEUM, Vol. V.

Plate LXIV.



CHARLES CHAUNCEY MELLOR

Born September 26, 1836: Died April 2, 1909

Fig. 8.—Charles Chauncey Mellor, Chairman of the Museum Committee, 1896–1909. (Photograph from the *Annals of Carnegie Museum*, 5:plate LXIV, 1909).

The matter of Hartman's vacation request is carried forward in Holland's next Monthly Report:

Mr. Hartman has requested leave of absence for three months in order to return to his home in Sweden, where he is required to be. I have granted his request with the understanding that his salary will be paid during two of the three months and will not be paid during the third month's absence. He is technically, as he avers, entitled to about two months absence, having never formally taken a vacation during the time he has been with us. (Holland Archives, Monthly Report of the Director to the Museum Committee, June 29, 1907).

Hartman left Pittsburgh about July 23 but spent time in New York City before departing for Sweden. On July 30, he sent Holland two letters on American Museum of Natural History letterhead, one being his Monthly Report of the Section for July. The other asked Holland to send twenty copies of the soon to be published *Memoirs* monograph to Sweden, so Hartman could distribute them to his European friends.

As Holland had stated, Hartman received no salary in October, the third month he was away. Holland verified that in his Monthly Report for September, within the context of another passage indicative of a strained relationship:

Mr. C. V. Hartman since his departure for Europe has not communicated in any way with the office of the Director, and the Director is without knowledge of his movements. He left here about the 23d of July. The understanding with him was that as he had no formal vacation since in our employment he would be allowed eight weeks on full pay, that if he extended his stay to three months, as he purposed doing, his salary for one month would be omitted. I propose, therefore, to omit drawing a warrant for him for this date. On the 1st of November, should he return during the coming month, we will resume the payment of his salary. (Holland Archives, Monthly Report of the Director to the Museum Committee, September 28, 1907).

In a letter from Sweden dated October 10, Hartman informed the Director that he would not be able to return to Pittsburgh before October 27, the extension being needed because of a severe case of tonsillitis, for which his physician in Sweden advised delaying his departure a few days. He finally arrived in Pittsburgh on October 30. The brief mention of his return by Holland was overly optimistic: "Professor C. V. Hartman returned from Sweden yesterday morning, and reported for duty. He appears to be in good health" (Holland Archives, Monthly Report of the Director to the Museum Committee, October 31, 1907). In actuality, Hartman's next three Monthly Reports of the Section of Ethnology and Archaeology disclose that he was ill from the "grippe" much of November and almost all of December 1907, resuming his work only in the latter half of January 1908. Hartman had been away from the Section for most of six months because of vacation and illness.

Apart from the comment in the Mellor letter about being in malarial regions, the reasons for Hartman's impaired health are not certain. The only photographs of him in Pittsburgh, taken in May 1907, the same month he wrote Mellor, depict a person who had gained considerable weight compared to images of him in Costa Rica in 1903 (Fig. 9). He experienced ill health after returning to Sweden, culminating in a medical leave of absence in 1923 (Lindblom, 1941; Watters and Fonseca Zamora, 2002a:276–277).

The fundamental issue underlying the strained relationship between Hartman and Holland was a difference of opinion about the primary purpose of the curatorial position (Watters and Fonseca Zamora, 2002a:282). Hartman tended to focus on field research, analysis of collections, and publications, whereas Holland emphasized acquisition of collections and preparation of exhibitions. These differing viewpoints are reflected in Hartman's two principal letters to Holland while negotiating for employment. The first letter, dated January 28, 1903 is filled with comments about research he had conducted previously in Mexico and Central America, and his "old plan" to resume that research. His second letter, of February 20, deals mainly with his practical museum experience and was a response to a specific request for that information, made by Holland on February 10 (Watters and Fonseca Zamora, 2001b). Holland's March 24 two-page letter of instruction directs Hartman to work with Pittier de Fabrega on collections of the Museo Nacional de Costa Rica (a task for which Carnegie Museum in turn was to receive duplicate artifacts), arrange for the purchase of the Velasco collection, make independent investigations to obtain ethnological and archaeological materials, and make collections of natural history specimens. Acquiring collections was the clear priority for Holland.



Fig. 9.—A. C. V. Hartman in 1903 at the Chinchilla site, Costa Rica (Section of Anthropology glass-plate negative G998, detail) B. Hartman in May 1907 at Powers Run Ravine near Pittsburgh (Carnegie Museum of Natural History Archives, Negative No. 4000; see Watters and Fonseca Zamora, 2001*b*:fig. 1, for a discussion of the particulars of this image).

Besides the differing ways they conceived and prioritized curatorial tasks, they also disagreed on what were acceptable field expenses and the relevance of comparative research at other museums. The problem of field expenses is evident in Hartman's letter to Mellor, but the issue of visiting other museums was not mentioned. However, museum visits were a major concern for Holland because they caused Hartman to be absent from his duties at Carnegie Museum, a situation that was exacerbated by his absences due to ill health. Holland referred to Hartman's museum visits when he stated, in his Monthly Report of May 31, that evidence of the accomplishments of these trips was "not very apparent to the Director." In the course of one protracted absence from December 1905 until March 1906, Holland became so annoyed that he ordered Hartman to return to Pittsburgh (Watters and Fonseca Zamora, 2002a:283–284).

Tension between administrators and curators about the place of anthropology in museums was by no means an unusual situation a century ago (Conn, 1998:75–113; Darnell, 1998:99–155). Holland and Hartman started having differences of opinion even before the start of the Costa Rica expedition, and this tension resurfaced in various ways in succeeding years. However, there is no doubt that events at Carnegie Museum in April and May, 1907, raised the level of tension to a new height, and ultimately led to Hartman's resignation a year later. The precipitating event was the dedication of the expanded Carnegie Institute building, which unleashed the Carnegie Museum staff's pent-up demand for resolutions to matters that had been held in abeyance. All documentation indicates that Holland chose not to be an advocate on Hartman's behalf with the Museum Committee, and the clear impression is that he made that choice deliberately. He did not propose to increase Hartman's salary, when he did so for four other staff members, nor is there any indication that he even considered endorsing any such action. Holland did not commit to writing any comments about Hartman's raise, but when he wrote about his vacation request, it was couched in less than flattering terms.

Hartman's commentary about Holland in the Mellor letter was carefully crafted to avoid direct accusation, yet it surely conveyed the impression of unfulfilled promises on Holland's part and more generally of some degree of miserliness on Carnegie Museum's part. One is left with the feeling that Hartman regarded himself, in view of his accomplishments, as poorly treated by Holland. He had put a lot of thought into structuring the content of that letter, had masterfully prepared his arguments, and had determined what to include and omit in supporting his case. To have Mellor and the Museum Committee refer the matter to Holland for action assuredly must have been perceived by Hartman, perhaps as the Committee intended, as the closing of the door on his curatorship at Carnegie Museum. One moreover is left with the impression that Hartman, knowing of the friendship of the Chairman and Director, already expected that outcome, had a contingency plan to become director of the Swedish Ethnographical Museum, set that scheme in motion by requesting his vacation from Holland, and came back to Carnegie Museum for six months merely to close down his museum anthropology career on this side of the Atlantic.

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whose efforts on behalf of Carnegie Museum have been for the most part forgotten today; Anthropology Collection Manager Deborah G. Harding for clarifying the exchanges arranged by Hartman; CMNH Librarian Bernadette Callery for assistance in accessing documents; Gerry Wagner for illustrating Figure 5; and Charmaine Steinberg for assistance with manuscript preparation.

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ON THE CRANIAL OSTEOLOGY OF THE SHORT-TAILED OPOSSUM
MONDELPHIS BREVICAUDATA (DIDELPHIDAE, MARSUPIALIA)

JOHN R. WIBLE

Curator, Section of Mammals

ABSTRACT

The Section of Mammals, Carnegie Museum of Natural History houses 54 partial and complete skulls of the short-tailed opossum *Monodelphis*. Described in detail and illustrated are the external surfaces of the bones of the skull for *M. brevicaudata* CM 52729 and the external and internal surfaces of one bone of the basicranium, the petrosal, for *Monodelphis* sp. CM 5024. The disposition of cranial foramina ranging in size from the foramen magnum to tiny emissary and nutrient foramina was studied in all 54 specimens, which in addition to 16 *M. brevicaudata*, includes four *M. dimidiata*, 29 *M. domestica*, two *M. osgoodi*, and three *Monodelphis* sp. Three categories of foramina were identified: (1) foramina bilaterally present in all specimens that show no significant variation; (2) bilateral and midline foramina present in all specimens that show variation in size, number, position, distinctness from other foramina, or elements contributing to their walls; and (3) foramina that are not present in all specimens that also vary in size, number, and position. Comparisons were made with four outgroups, the didelphid *Didelphis albiventris*, the dasyurid *Dasyurus maculatus*, the early Paleocene metatherian *Pucadelphys andinus*, and the Late Cretaceous eutherian *Zalambdalestes lechei*, in order to evaluate the foramina of *Monodelphis* in a phylogenetic context. Of the foramina considered here, four distinguish *Monodelphis*; three distinguish Didelphidae; 15 distinguish Marsupialia; nine distinguish Metatheria; and seven occur across Theria.

KEY WORDS: *Monodelphis*, Didelphidae, Marsupialia, skull, osteology, foramina

INTRODUCTION

Until recently, the bulk of the evidence for our understanding of the basal radiations of marsupial mammals consisted of teeth and jaws (Clemens, 1979). The last few years have witnessed the discovery of well-preserved skulls and even skeletons of basal members of Metatheria (Marshall and Muizon, 1995; Muizon, 1998; Rougier et al., 1998). Didelphidae, the New World opossums, is the extant marsupial family that from a phylogenetic standpoint is generally considered to provide the most appropriate model for studying the anatomy and biomechanics of these basal forms (Wible, 1990; Argot, 2001). However, few detailed, well-illustrated treatments of the didelphid skull or for that matter of any extant marsupial skull are available. In fact, perhaps the most complete description and illustration of a metatherian skull is that of *Pucadelphys andinus* from the early Paleocene of Bolivia (Marshall and Muizon, 1995), referred to Didelphidae by its describers. It is the dearth of similar treatments for extant marsupials that is the impetus for this report. A second impetus is the opportunity to review and standardize anatomical terminology.

A sizeable literature on aspects of didelphid anatomy does exist, with the most comprehensive single source on the didelphid skull likely being Coues (1872), which unfortunately is poorly illustrated and uses terminology that is out of date. Another noteworthy general contribution is the anatomical photographic atlas by Ellsworth (1976), but unfortunately the quality and clarity of the published photographs are uneven, and few features are labelled. More recently, Macrini (2000), in an unpublished masters' thesis, has described the anatomy of the internal surfaces of the skull (e.g., braincase, nasal cavity) of *Monodelphis domestica* based on CT scans; external views of the skull produced from the

CT scans are published in Macrini (2002:fig. 4). Selected anatomical topics of the didelphid head that have received considerable attention include the basicranium (e.g., Archer, 1976; Maier, 1989; Wible, 1990; Sánchez-Villagra and Wible, 2002) and cranial musculature (e.g., Hiiemae and Jenkins, 1969; Turnbull, 1970; Minkoff et al., 1979). There is also a sizeable literature on aspects of cranial ontogeny in didelphids (e.g., Toeplitz, 1920; Nesslinger, 1956; Maier, 1987a, b; Filan, 1991; Clark and Smith, 1993; Smith, 1994; Rowe, 1996; Abdala et al., 2001; Sánchez-Villagra et al., 2002).

Two didelphids, *Didelphis virginiana* and *Monodelphis domestica*, have become increasingly popular as laboratory models for biomedical research (Tyndale-Biscoe and Janssens, 1988; Saunders and Hind, 1997). Because the latter taxon has been the subject of most recent contributions on aspects of cranial development (e.g., Maier, 1987a, b; Filan, 1991; Clark and Smith, 1993; Smith, 1994), the genus *Monodelphis* was chosen to be the subject of this report, a bone-by-bone description of the exterior of the adult skull. For illustrative purposes, a skull from another species of the genus, *M. breviceaudata*, was chosen for the bulk of the figures. Differences between *M. breviceaudata*, *M. domestica*, and two other species, *M. dimidiata* and *M. osgoodi*, are noted. Fifteen species of *Monodelphis* are recognized by Gardner (1993).

MATERIALS AND METHODS

The Section of Mammals of the Carnegie Museum of Natural History has holdings of 54 skulls of *Monodelphis*, including 16 *M. breviceaudata*, 29 *M. domestica*, 4 *M. dimidiata*, 2 *M. osgoodi*, and 3 *M. sp.* All specimens were examined for this report (see Appendix 1). Three cranial measurements (premaxillary-condylar length, maximum zygomatic breadth, and length of mandible) were taken from 47 of the 54 specimens (see Appendix 2); the remaining seven specimens were damaged in some way, but it was possible to take at least one of these measurement (length of mandible) from them. Regarding age of the specimens, the majority (45 of 54) has all four upper and lower molars in place in the jaws and are considered to be adults. In the remainder, the deciduous third premolar is retained with either the ultimate or penultimate molar not fully erupted (see Appendix 2); these specimens are considered to be juveniles. The third premolar is the only tooth to be replaced in marsupials (Luckett, 1993).

The bone-by-bone descriptions of the exterior of the adult skull are based principally on *Monodelphis breviceaudata* CM 52729, the specimen illustrated in figures 1–6, and 9. The chief exception is the petrosal bone, which is based on an isolated left petrosal of *Monodelphis* sp. CM 5024 (which I provisionally have identified as *M. domestica*) and an isolated right petrosal of *M. breviceaudata* CM 5061; the former is illustrated in figures 7–8. Following the bone-by-bone descriptions is a discussion of the major cranial foramina, their contents, the variations observed among the available sample, and the condition observed in selected outgroups. The descriptions and discussions touch upon some soft-tissue structures of the head, specifically, muscles, nerves, arteries, and veins. The two principal sources for information on soft tissues are the literature (e.g., Tandler, 1899; Hiiemae and Jenkins, 1969; Turnbull, 1970), including some references by the author (e.g., Wible, 1987, 1990; Wible and Hopson, 1995), and unpublished observations based on the study of serially sectioned specimens. The principal collections that house embryological series of marsupials studied by me are as follows: Anatomy Unit, University of Wales, Cardiff, United Kingdom; Duke University Comparative Embryological Collection, Durham, North Carolina; Lehrstuhl für Spezielle Zoologie, Eberhard-Karls-Universität, Tübingen, Germany; and Zentrum der Morphologie, Johann-Wolfgang-Goethe-Universität, Frankfurt am Main, Germany.

Unfortunately, morphologists that have published on the cranial anatomy of extinct and extant metatherians have not employed a common terminology for their descriptions. The reasons for this are many, but largely are the result of history and of unresolved homologies. As a step toward a standardized terminology, Appendix 3 details the sources for the non-dental anatomical terms employed. Whenever possible, the Latin term (or anglicized version thereof) from the fourth edition of the *Nomina Anatomica Veterinaria* (1994) has been used. For the dentition, the abbreviations “I, C, P, M” and “i, c, p, m” are used to refer to upper and lower incisors, canines, premolars, and molars, respectively.

Institutional Abbreviations

AMNH	Department of Mammalogy, American Museum of Natural History, New York, New York.
CM	Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

FMNH	Division of Mammals, Field Museum, Chicago, Illinois.
UKMNH	Division of Mammals, University of Kansas Natural History Museum, Lawrence, Kansas.
WAM	Western Australian Museum, Perth.

DESCRIPTIONS

The cranium of *Monodelphis brevicaudata* CM 52729 is drawn in dorsal, lateral (with and without zygoma), ventral, and occipital views (Figs. 1–2, 4–6, 9) and the mandible in lateral and occlusal views (Figs. 2–3). In addition, the left petrosal of *M. sp.* CM 5024 is drawn in ventral, dorsal, and lateral views (Figs. 7–8). Other useful illustrations of *Monodelphis* already in the literature include line drawings of the cranium of *M. brevicaudata* AMNH 130516 in dorsal, lateral, and ventral views (Novacek, 1993:fig. 9.4), stipple drawings of the right braincase and lower jaw of *M. domestica* in lateral and ventral views (Maier, 1989:fig. 1), stereophotographs of the basicranium of *M. dimidiata* WAM M6824 in ventral and oblique ventral views (Archer, 1976:plate 6A, B), stipple drawings of the right ear region of *M. scalops* (Maier, 1989:fig. 2), and stipple drawings of the right petrosal of *M. sp.* AMNH 133248 in ventral and lateral views (Sánchez-Villagra and Wible, 2002:figs. 3b and 5d).

Nasal

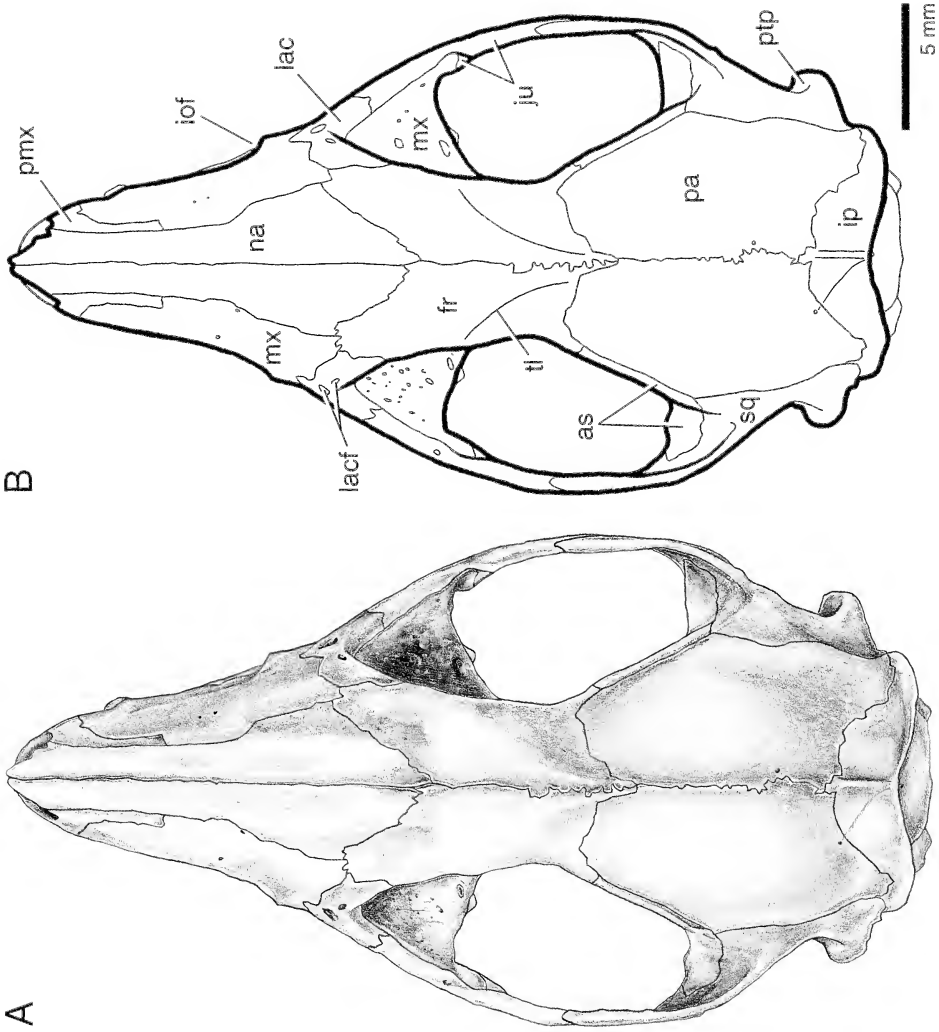
The paired nasal bones occupy the dorsum of the snout and contribute to the dorsal border of the external nasal aperture (Figs. 1–2).

In dorsal view (Fig. 1), the nasals contact, from anterior to posterior, the premaxillae, maxillae, and frontals. The nasals extend from the tip of the rostrum to the level of the M3, a little behind the anterior orbital rim. The rostral two-thirds of the paired nasals are narrow, with essentially parallel sides; the posterior one-third is somewhat diamond-shaped, achieving its maximum width just rostral to the frontomaxillary suture. The frontals overlap the nasals and produce a roughly V-shaped suture. In lateral view (Fig. 2), the anterior nasal spine is well developed, resulting in a considerable nasal overhang of the external nasal aperture. Although the nasal's rim on the external nasal aperture is curved (Fig. 1), there is no anterior nasal notch as occurs in some other taxa (e.g., the Late Cretaceous eutherian *Zalambdalestes*, Wible et al., in press). There are no foramina in the nasals.

Premaxilla

The paired premaxillae are small elements that contain the alveoli for the five upper incisors and, along with the nasals, form the tip of the rostrum (Fig. 2). The premaxillae contact the nasals dorsally and the maxillae posteriorly. The alveolar processes of the premaxillae contain the incisors. The facial processes of the left and right premaxillae form the floor and side walls of the external nasal aperture, the roof being formed by the nasals. The palatal processes of the premaxillae form most of the border for the large incisive foramina (Fig. 5).

In lateral view (Fig. 2), the dorsoventral dimension of the rostral tip of the facial process is very short, and the included root of the I1 must also be short. Posterior to the rostral tip, the dorsoventral dimension increases gradually to its maximum at the level of the I5. The bulk of the contact of the posterior border of the facial process with the maxilla is vertical, starting ventrally just behind the I5 alveolus (to which the maxilla makes a very small contribution posterolaterally). As this suture nears the nasal bone, there is a finger-like projection of the premaxilla (the posterodorsal process) interposed between the maxilla and nasal that reaches to just behind the level of the canine. There is a minute nutrient foramen



bilaterally present in the facial process dorsal to the I3–4 embrasure, near the rim of the external nasal aperture.

In ventral view (Fig. 5), the alveolar and palatal processes of the premaxilla form approximately one-fifth the length of the hard palate. Of the upper five incisors, the I1 alveolus is the largest and just off the midline; the right and left I1 are angled toward each other and their crowns contact. I1 and I2 are separated by a diastema. From the I2 through I5, there is a slight size increase in tooth size; the alveoli are very close and the crowns contact. Behind the I5 is a large depression for the tip of the lower canine. The lateral wall and posterolateral part of the depression are formed by the maxilla, and the remainder by the premaxilla. The posteromedial border of the depression, which is premaxilla, also forms the anteromedial border of the alveolus of the upper canine. The most noteworthy structure in the palatal process is the large, finger-like incisive foramen, which lies medial to the alveoli of I3–5 and the depression for the lower canine. The bulk of this foramen is within the premaxilla; the maxilla forms the posterior border, which is somewhat U-shaped. Forming the foramen's medial border is the medial palatine process of the premaxilla, which increases slightly in breadth posteriorly. Visible through the incisive foramen is the maxilloturbinal.

Maxilla

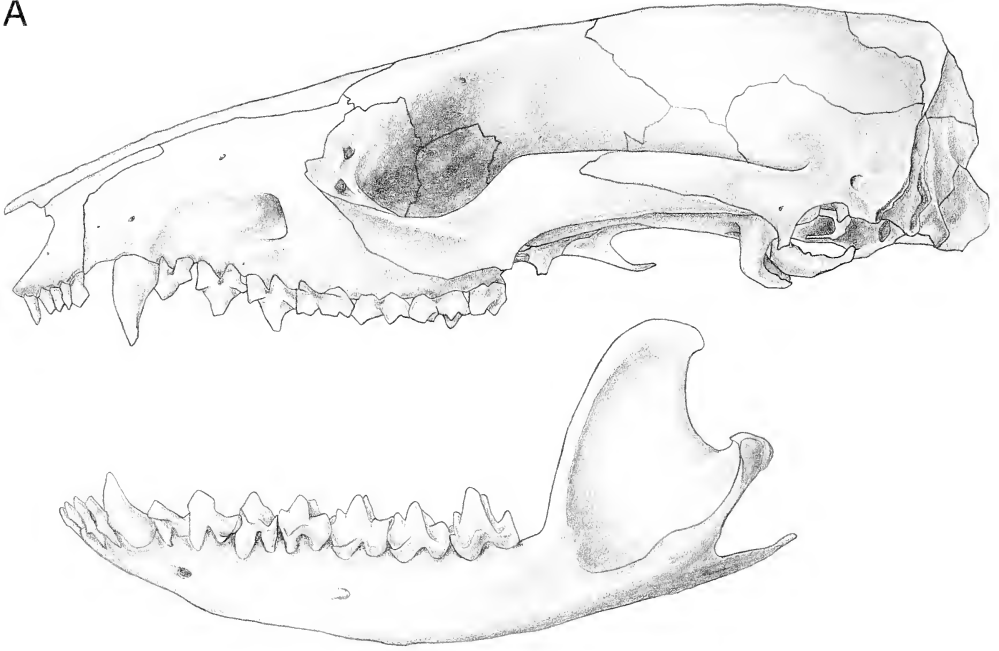
The paired maxillae are the major elements of the lateral wall of the snout and hard palate, and contain the alveoli for the canine and seven postcanine teeth (three premolars and four molars). On the face (Fig. 2), the maxilla contacts the premaxilla anteriorly and dorsally, the nasal and frontal dorsally, and the lacrimal and jugal posteriorly. On the palate (Fig. 5), the maxilla contacts the premaxilla anteriorly and the palatine posteromedially. The maxilla also contributes to the anterior floor of the orbit.

On the face (Fig. 2), the sutures with the premaxilla and nasal have been described above. Posterodorsally, at the level of the M1–M2 embrasure, the maxilla contacts the frontal at a narrow, irregular suture. Ventral to this, the maxilla contacts the lacrimal and then the jugal at gently curved sutures, although that with the lacrimal includes a small, V-shaped process of the maxilla at the level of the upper lacrimal foramen. The most conspicuous feature on the facial process of the maxilla is the large infraorbital foramen. In lateral view, it is a roughly U-shaped aperture, open rostrally, with the base of the U dorsal to the P3–M1 embrasure; in anterior view it is subcircular. Also prominent is the large root of the upper canine, which is visible through the thin bone. It is gently curved, extending posteriorly behind the level of the anterior root of P2 and dorsally above the level of the upper lacrimal foramen. There are also several small nutrient foramina on the face, with the most conspicuous ones posterodorsal and anterior to the canine root, along the course of the nasolacrimal duct, also partially visible through the thin bone.

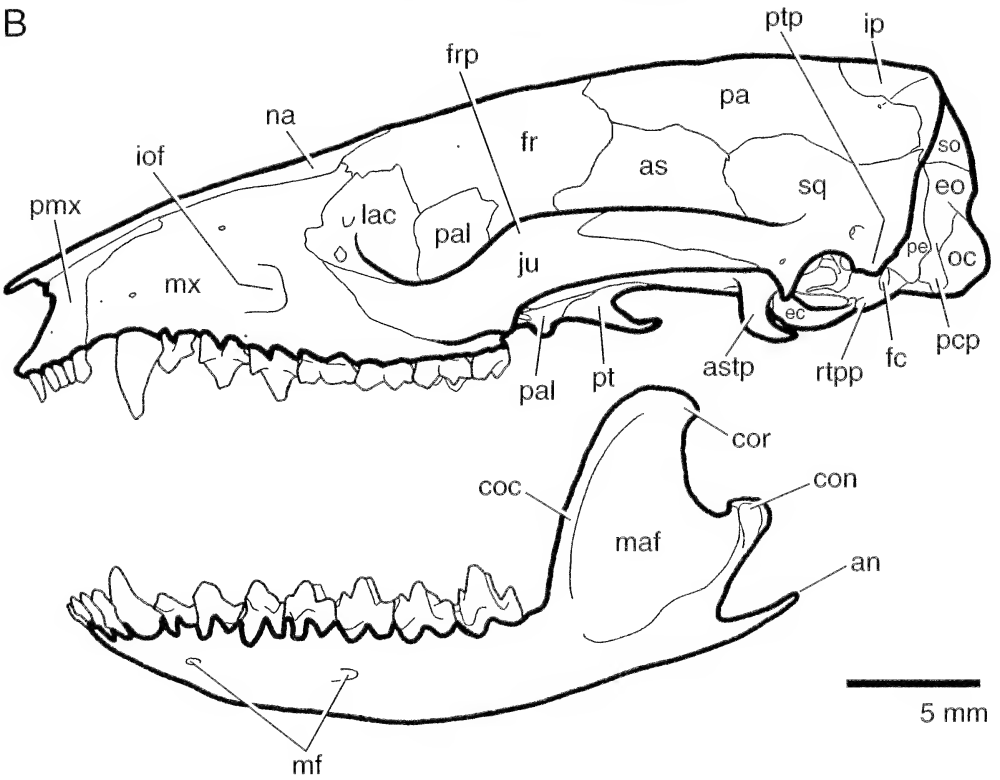
On the palate (Fig. 5), the suture with the premaxilla has been described above. The intermaxillary suture extends from the level of the canine to the M2 metacone and has a slightly raised crest, more evident posteriorly. The palatines' contribution to the hard palate is small and roughly square, and so the maxilla contacts the palatine at longitudinal and horizontal sutures. The longitudinal suture begins posteriorly in the anteromedial

Fig. 1.—*Monodelphis brevicaudata* CM 52729, dorsal view of skull (A) with accompanying line drawing (B). Abbreviations: **as**, alisphenoid; **fr**, frontal; **iof**, infraorbital foramen; **ip**, interparietal; **ju**, jugal; **lac**, lacrimal; **lacf**, lacrimal foramen; **mx**, maxilla; **na**, nasal; **pa**, parietal; **pmx**, premaxilla; **ptp**, posttympanic process; **sq**, squamosal; **tl**, temporal line.

A



B



border of the minor palatine foramen and runs more or less forward to the level of the M2 metacone. It turns medially into the horizontal suture, which is interdigitated, with the processes of the palatine reaching nearly to the level of the M2 protocone. The lateral part of the horizontal suture is open, with the palatine forming the posterior border of the elongate major palatine foramen or maxillopalatine vacuity, the most conspicuous feature on the hard palate. The major palatine foramen extends between the level of the P3–M1 and M2–M3 embrasures. Running forward from the anterior edge of the major palatine foramen is a broad, shallow groove for the foramen's contents that reaches nearly to the level of the back of the canine. The minor palatine foramen is oval, on the maxillopalatine suture, posteromedial to M4, and faces anteromedially. The posterolateral border of the foramen is formed by very thin processes of the maxilla and palatine.

The anterior root of the zygoma is formed by the short zygomatic process of the maxilla (Fig. 5). The anterior edge of this process is opposite the M2–M3 embrasure and the posterior edge opposite the M4 paracone. The zygomatic process of the maxilla sends a small lappet posteriorly a short distance along the inner surface of the jugal (Fig. 1). In *Didelphis*, the maxilla has a distinct protuberance dorsal to M4 for attachment of the superficial masseter muscle (Hiiemae and Jenkins, 1969; Turnbull, 1970). Such a distinct protuberance is lacking in CM 52729.

The portion of the maxilla housing the roots for M2–4 forms the wedge-shaped floor of the orbit (Fig. 1). In fact, the tips of the medial roots of M3 and 4 are exposed in the orbital floor. The contacts of the maxilla in the orbital floor are with the anterior process of the alisphenoid posteromedially, the palatine medially, the lacrimal anterolaterally, and the jugal laterally (Fig. 4). The maxilla forms the floor and lateral wall of the maxillary foramen, the posterior opening into the infraorbital canal, which is not visible in lateral view. The roof and medial wall of the maxillary foramen are completed by the lacrimal, with a thin sliver of palatine interposed between the maxilla and lacrimal medially.

Palatine

The paired palatine bones have a horizontal process that forms roughly the posterior one-third of the hard palate (Fig. 5) and a perpendicular process that contributes to the medial orbital wall and to the roof and walls of the choanae (Fig. 4).

As noted above with the maxilla, the horizontal processes of the palatines are roughly square and have longitudinal and horizontal sutures with the maxillae (Fig. 5). Because of the thinness of the palatine, it is evident that the palatine overlaps the maxilla along the posterior four-fifths of the longitudinal suture and along the medial one-third of the horizontal suture. Both sutures border sizeable foramina on the hard palate. In the posterior longitudinal suture is the minor palatine foramen, approximately half of which is formed by the palatine in ventral view. In the lateral horizontal suture is the major palatine foramen or maxillopalatine vacuity, of which the palatine forms only the narrow posterior border. Medial to the minor palatine foramen on the right side is a tiny aperture in the palatine that may represent an accessory palatine foramen; the left side has two tiny apertures, both of

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Fig. 2.—*Monodelphis brevicaudata* CM 52729, left lateral view of skull including mandible (A) with accompanying line drawing (B). Abbreviations: **an**, angular process; **as**, alisphenoid; **astp**, alisphenoid tympanic process; **coc**, coronoid crest; **con**, mandibular condyle; **cor**, coronoid process; **ec**, ectotympanic; **eo**, exoccipital; **fc**, fenestra cochleae; **fr**, frontal; **frp**, frontal process of the jugal; **iof**, infraorbital foramen; **ip**, interparietal; **ju**, jugal; **lac**, lacrimal; **maf**, masseteric fossa; **mf**, mental foramen; **mx**, maxilla; **na**, nasal; **oc**, occipital condyle; **pa**, parietal; **pal**, palatine; **pcp**, paracondylar process of the exoccipital; **pe**, petrosal; **pmx**, premaxilla; **pt**, pterygoid; **ptp**, posttympanic process; **rtpp**, rostral tympanic process of the petrosal; **so**, supraoccipital; **sq**, squamosal.

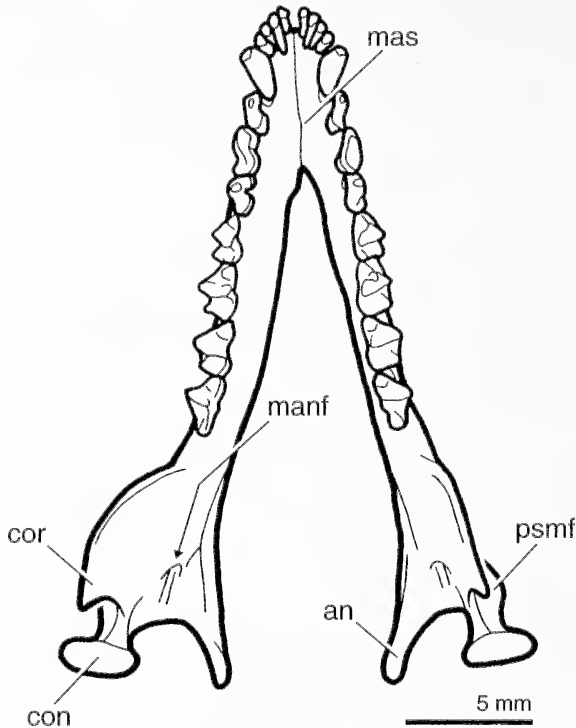


Fig. 3.—*Monodelphis brevicaudata* CM 52729, line drawing of left and right mandibles in occlusal view. Abbreviations: **an**, angular process; **con**, mandibular condyle; **cor**, coronoid process; **manf**, mandibular foramen; **mas**, mandibular symphysis; **psmf**, posterior shelf of the masseteric fossa.

which are slightly more medially positioned than on the right side. As noted above with the intermaxillary suture, the interpalatine suture has a raised crest that in the case of the palatine runs the length of the suture. This crest turns laterally along the posterior border of the horizontal process to form the low postpalatine torus that extends to the minor palatine foramen. Posteromedial to the minor palatine foramen is a small foramen through the postpalatine torus, connecting the hard palate and choanae; this foramen is visible in occipital view (Fig. 9). It likely transmitted structures from the minor palatine foramen to the soft palate.

The lateral surface of the perpendicular process of the palatine lies in the anterior half of the orbitotemporal fossa (Fig. 4). From anterior to posterior, it contacts the lacrimal, frontal, and orbitosphenoid along its dorsal surface, and the maxilla, alisphenoid, pterygoid, and presphenoid along its ventral surface. It is tallest posterior to the lacrimal where it forms roughly the ventral three-fourths of the medial orbital wall, the frontal completing the dorsal fourth. Extending anteriorly and posteriorly from the base of this tallest part of the palatine are narrow anterior and posterior processes. The shorter anterior process extends between the lacrimal and maxilla into the maxillary foramen to the level of the M1–M2 embrasure; the maxillary foramen is at the level of the M2 centrocrista. The posterior process extends into the floor of the sphenorbital fissure, where it contacts the presphenoid and orbitosphenoid. At a level dorsal to the M3–M4 embrasure near the suture with the maxilla, the palatine is pierced by a large, anteromedially directed sphenopalatine foramen. U-shaped in lateral view, in oblique posterolateral view this aperture appears nearly dumbbell shaped, with two foramina merged. Presumably the anterolateral foramen

transmits the sphenopalatine vessels and branches of the maxillary nerve to the hard palate and the posteromedial foramen transmits the caudal nasal nerve and vessels to the nasal cavity. Immediately posterior to the sphenopalatine foramen is a tiny, anterolaterally directed foramen of uncertain function. More posteriorly are three openings that connect the orbital fossa with the choanae. The smaller two are entirely within the palatine: one at the level of the anterior edge of the ethmoidal foramen and the other anterodorsal to that near the suture with the frontal. The largest is elongate, irregular, and situated posterior to the palatine, between that bone and the pterygoid. It is an unossified area that is closed off in some other specimens (e.g., CM 52730, 76730).

The medial surface of the perpendicular process of the palatine forms the lateral wall and contributes to the roof of the choanae (Fig. 5), and extends rostrally into the nasal fossa. At the choanae, the palatine's posterior border is V-shaped and in contact with the pterygoid bone, except along the V's medial leg where the suture contains the irregular opening described above. Along the midline, the palatine abuts the narrow presphenoid bone.

Lacrima

The paired lacrimal bones form the anterior rim of the orbit and have facial, orbital, and zygomatic processes (Fig. 4).

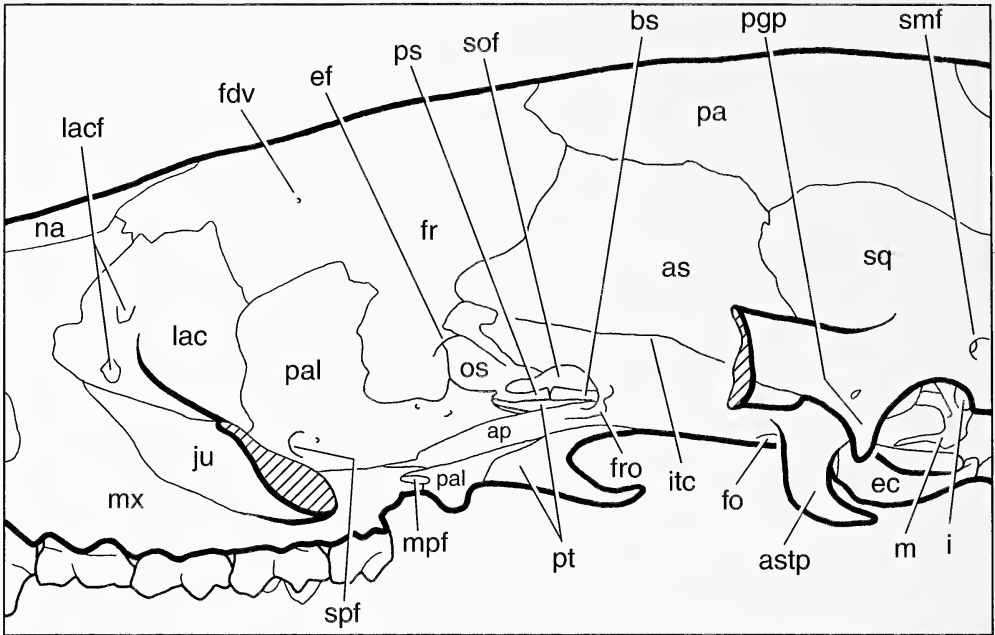
The narrow facial process of the lacrimal is roughly crescentic, but at a level dorsal to the infraorbital foramen is a small tongue-shaped process that is directed anterodorsally (Figs. 1, 4). Contacts of the facial process are with the frontal dorsally, the maxilla anteriorly, and the jugal ventrally. Posteroventrally, the facial process narrows to a short zygomatic process that extends posterolaterally dorsal to the jugal to the level of the M2 metacone (Fig. 4). Two lacrimal foramina lie within the facial process (Figs. 1, 4): the larger anteroventral foramen is immediately dorsal to the jugal suture and is directed anteromedially; the smaller posterodorsal foramen is opposite the top of the tongue shaped process described above and is directed ventrally. The rim of the orbit is rounded and not marked by a distinct crest, except for a portion on the jugal bone behind the zygomatic process of the lacrimal.

The larger orbital process of the lacrimal forms nearly the entire anteromedial wall of the orbit (Fig. 4), the exception being a small slip of palatine that completes the wall inferiorly. In the anteromedial orbital wall, the orbital process of the lacrimal contacts the frontal and palatine posteriorly, and the palatine inferiorly. The orbital process also forms the medial wall and roof of the maxillary foramen; the remaining borders are formed by the maxilla and palatine. Extending posterolaterally from the dorsolateral aspect of the maxillary foramen is the short zygomatic process of the lacrimal, which contacts the maxilla ventrally and the jugal posteriorly. Dorsal to the maxillary foramen on the right side of CM 52729 is a small, anteriorly directed foramen of uncertain function in the orbital process of the lacrimal; on the left side are two smaller foramina rather than a single opening.

Jugal

The paired jugal bones are the principal elements of the zygomatic arches, completing the gap between the zygomatic processes of the maxilla and lacrimal anteriorly and of the squamosal posteriorly (Fig. 2). The jugal also contributes to the ventral rim of the orbit and the face above the upper molars. It extends from the level of the M1 centrocrista anteriorly to the glenoid fossa posteriorly.

The portion of the jugal on the face lies dorsal to the upper molars and with the maxilla forms the anterior root of the zygomatic arch (Fig. 2). In lateral view (Fig. 4), the jugal contacts the maxilla inferiorly at a roughly crescentic suture and the zygomatic process of the lacrimal bone anterodorsally. The surface of the jugal on the face bears a large muscular



5 mm

Fig. 4.—*Monodelphis brevicaudata* CM 52729, line drawing of left orbitotemporal region without zygoma (parallel lines represent cut surfaces). Abbreviations: **ap**, anterior process of the alisphenoid; **as**, alisphenoid; **astp**, alisphenoid tympanic process; **bs**, basisphenoid; **ec**, ectotympanic; **ef**, ethmoidal foramen; **fdv**, foramen for the frontal diploic vein; **fr**, frontal; **fro**, foramen rotundum; **fo**, foramen ovale; **i**, incus; **ju**, jugal; **lac**, lacrimal; **lacf**, lacrimal foramen; **m**, malleus; **mpf**, minor palatine foramen; **mx**, maxilla; **na**, nasal; **os**, orbitosphenoid; **pa**, parietal; **pal**, palatine; **pgp**, postglenoid process; **ps**, presphenoid; **pt**, pterygoid; **smf**, suprameatal foramen; **sof**, sphenorbital fissure; **spf**, sphenopalatine foramen; **sq**, squamosal.

depression that extends anteriorly onto the maxilla posterior to the infraorbital foramen. This cigar-shaped depression houses the zygomaticus and levator labii muscles, based on *Didelphis marsupialis* (Turnbull, 1970). Behind the lacrimal, the dorsal border of the jugal is curved to form the infraorbital margin, which ends posteriorly in a low, but distinct frontal process (dorsal process) providing attachment for the postorbital ligament delimiting the orbital and temporal fossae (Fig. 2). Behind the frontal process in lateral view, the jugal contacts the zygomatic process of the squamosal at a V-shaped suture, the legs of which are posteriorly directed. The superior leg is very short, but the inferior leg reaches all the way to the glenoid fossa. The suture between the jugal and squamosal on the medial surface of the zygoma is diagonal, slanted anterodorsally, and more posteriorly placed. Beginning anteriorly on the zygomatic process of the maxilla and extending nearly to the glenoid fossa is a narrow muscular depression on the inferior margin of the jugal's lateral surface, which is for the superficial and deep masseter, based on *Didelphis* (Hiemae and Jenkins, 1969; Turnbull, 1970). The medial surface of the zygomatic arch, including the maxillary, jugal, and squamosal contributions, is concave and provides attachment anteriorly for the zygomaticomandibularis muscle and posteriorly for the zygomatic part of the temporalis muscle, based on *Didelphis marsupialis* (Turnbull, 1970). In ventral view (Fig. 5), the ventral edge of the jugal bears a blunt crest from the anterior root of the zygoma to just anterior to the glenoid fossa. At the glenoid, the jugal widens to form a broad glenoid

process (Fig. 6). The posterior surface of the glenoid process bears a facet that contributes to the anterolateral corner of the glenoid fossa. The glenoid process of the jugal approximates but does not touch the glenoid process of the alisphenoid.

Frontal

The paired frontal bones form the skull roof medial to the orbits (Fig. 1) and contribute to the medial walls of the orbital and temporal fossae (Fig. 4).

In dorsal view in the skull roof (Fig. 1), the frontals contact the nasals anteriorly at a roughly V-shaped suture, the legs of which are directed anteriorly. Lateral to the frontonasal suture, the anterior edge of the frontal has a narrow contact with the maxilla and the lacrimal. The thinness of the bone shows that the frontal overlaps both the maxilla and lacrimal. Posterior to the lacrimal, the frontal forms the rounded supraorbital margin, the posterior limit of which is indicated by a subtle postorbital process at the anterior end of the temporal line. From the postorbital process, the low temporal line curves posteromedially on the frontal, converging with its member of the opposite side at the frontoparietal suture to form a trace of a sagittal crest. The posterior edge of the frontal has a broad contact with the parietal and, lateral to that, a narrow contact with the alisphenoid. On the midline, a small V-shaped process of the frontals is interposed between the parietals. Because of the thinness of the bone, it is evident that the parietal and alisphenoid considerably overlap the frontal at their sutures. The anterior half of the interfrontal suture is relatively straight, but its posterior half is sinuous.

In lateral view within the orbital and temporal fossae (Fig. 4), the contacts of the frontal from anterior to posterior are with the lacrimal, palatine, orbitosphenoid, and alisphenoid. The suture with the lacrimal within the orbit is roughly vertical and that with the palatine is initially horizontal, then vertical, and then horizontal again. The latter two portions of the frontopalatine suture delimit the ventralmost intrusion of the frontal into the orbitotemporal fossa. Posterior to the frontopalatine suture, the frontal contacts the orbitosphenoid at a short vertical suture, at the top of which the ethmoidal foramen lies, and then at a short concave suture. Posterior to the suture with the orbitosphenoid, the frontal has a very broad contact with the overlapping alisphenoid that trends posterodorsally.

Two foramina are associated with the frontal within the orbitotemporal fossa (Fig. 4). First, wholly within the frontal in the supraorbital margin, anterior to the subtle postorbital process is a small, anterolaterally directed aperture, which I interpret as a foramen for the frontal diploic vein. Second, in the middle of the suture between the frontal and orbitosphenoid lies the ethmoidal foramen. This large oval aperture is nearly vertically directed, and, therefore, only its lateral rim is visible in lateral view. The frontal and orbitosphenoid contribute equally to the borders of the ethmoidal foramen, with the frontal forming the anterior and most of the lateral walls and the orbitosphenoid forming the posterior and most of the medial walls.

The frontal in *Didelphis marsupialis* has a distinct orbitotemporal crest that runs posteroventrally from the postorbital process to the ethmoidal foramen and marks the anterior extent of the origin of the temporalis muscle (Turnbull, 1970). An orbitotemporal crest is not evident in CM 52729.

Parietal

The paired parietals form the bulk of the posterior skull roof (Fig. 1) and arch over the cerebral hemispheres to contribute to the posterior side wall of the braincase (Fig. 2). They also provide the bulk of the attachment area for the temporalis muscle, based on *Didelphis* (Hiemae and Jenkins, 1969; Turnbull, 1970).

The parietal extends from the level of the sphenorbital fissure anteriorly to just in front of the nuchal crest posteriorly (Fig. 1). The thinness of the bone in the posterior skull roof reveals the details of the interosseous contacts. Along its anterior and posterior margins, the parietal overlaps considerably the frontal and interparietal, respectively. Laterally, the parietal is overlapped considerably by the alisphenoid and squamosal. The suture between the parietals, which lies in the low sagittal crest, is relatively straight anteriorly but tightly interdigitated posteriorly. There are several tiny emissary foramina in or near the posterior part of the suture. The largest, shown in Figure 1, is in the right parietal anterior to the interparietal bone. In the left parietal is a small, more laterally situated foramen, just anterior to the interparietal bone. It is directed posterodorsomedially into a groove that extends nearly to the confluence of the sagittal and nuchal crests, mainly on the interparietal bone. This foramen and groove do not exist on the right side, but a corresponding structure (presumably a vascular canal with no external egress) is visible because of the thinness of the parietal and interparietal.

Interparietal

An unpaired, intramembranous interparietal (postparietal) bone is described in postnatal stages of *Monodelphis domestica* by Clark and Smith (1993) and of *Didelphis marsupialis* by Toeplitz (1920). This bone apparently fuses seamlessly with the more posteriorly positioned supraoccipital along the nuchal crest and, therefore, is often labelled in adult didelphids as part of the supraoccipital (e.g., Hershkovitz, 1992:figs. 18, 19; Novacek, 1993:fig. 9.4). With little exception, the adult *Monodelphis* studied here have no indication of a suture separating the interparietal and supraoccipital. There are two juvenile *M. domestica* CM 80019 and 80020 (see Appendix 2), which show an open seam between a small portion of the contact between the interparietal and supraoccipital along the occipital surface of the nuchal crest. This seam can be followed only a short distance dorsal to the mastoid exposure of the petrosal. An even shorter seam immediately dorsal to the mastoid exposure is visible on the right side only of *M. brevicaudata* CM 63510, an adult with fully erupted M4. Based on the ontogenetic reports and on these specimens, I accept that the midline bone lying posterior to the parietal and forming the bulk of the nuchal crest in *Monodelphis* is the interparietal.

In dorsal view in CM 52729 (Fig. 1), the interparietal is shaped somewhat like a moustache. Clear sutures distinguish the interparietal from the parietals and squamosals, but there is no separation from the supraoccipital. The anterior surface of the interparietal contacts the paired parietals. In fact, because of the thinness of the parietals, it is very evident that they overlap the interparietal to a considerable extent. The lateral tips of the interparietal have a narrow contact with the posterodorsal squama of the squamosal. Based on the juveniles, the posterior surface of the interparietal forms the bulk of the nuchal crest and its contact with the supraoccipital lies on the occipital side of the nuchal crest. Also based on the juveniles, it seems likely that posteroventrally, the interparietal had a very narrow contact with the mastoid exposure of the petrosal. On the midline of the interparietal is a distinct, but low sagittal crest, which is better developed than that on the parietals.

Pterygoid

The medial surfaces of the paired pterygoid bones form most of the roof and lateral walls of the nasopharyngeal passage behind the choanae (Fig. 5). The lateral surface of the pterygoid is exposed in the infratemporal fossa and makes a tiny contribution to the orbital mosaic (Fig. 4).

In ventral view (Fig. 5), for descriptive purposes, I divide the pterygoid into two portions: one in the roof and a second in the lateral wall of the nasopharyngeal passage (the entopterygoid crest of Novacek, 1986); these have a narrow connection at the level of the presphenoid-basisphenoid suture. The portion in the roof is anteroposteriorly elongate, roughly cigar-shaped with pointed rather than rounded ends, and lies lateral to the midline. The posterior half underlies the basisphenoid. The anterior half does not underlie another bone; it contacts the presphenoid and basisphenoid medially and is separated from the palatine by an irregular fissure anterolaterally. At the posterolateral edge is a small aperture between the pterygoid and basisphenoid that represents the posterior opening of the pterygoid canal (Fig. 6). Leading to this aperture from behind is a narrow groove on the basisphenoid that can be traced posteriorly between the carotid foramen and the transverse canal foramen.

The portion of the pterygoid in the lateral wall of the nasopharyngeal passage, the entopterygoid crest, is boomerang-shaped with superior and inferior arms that meet at a roughly 45° angle (Fig. 4). The flat superior arm connects to the portion of the pterygoid in the nasopharyngeal roof (Fig. 5) and from that connection runs anteroventrolaterally with the superior aspect of its lateral surface in contact with the alisphenoid and palatine; the inferior aspect does not contact another bone. The superior arm joins the inferior arm posterodorsal to the back of the hard palate. The freestanding inferior arm extends posteriorly into the infratemporal fossa and curves slightly laterally. It is flat proximally, but ends in a thickened, rounded hamular process that has a distinct lateral bend, presumably to accommodate the tendon of the tensor veli palatini muscle. The inferior arm is frequently damaged in museum specimens; it is broken on the right side of CM 52729 and wholly missing on the left side (as apparently is the case in the *Monodelphis breviceaudata* AMNH 130516 illustrated by Novacek, 1993:fig. 9.4B, C). It is from the lateral surface of the pterygoid and adjacent parts of the alisphenoid and palatine that the internal pterygoid muscle arises, based on *Didelphis* (Hiemae and Jenkins, 1969; Turnbull, 1970).

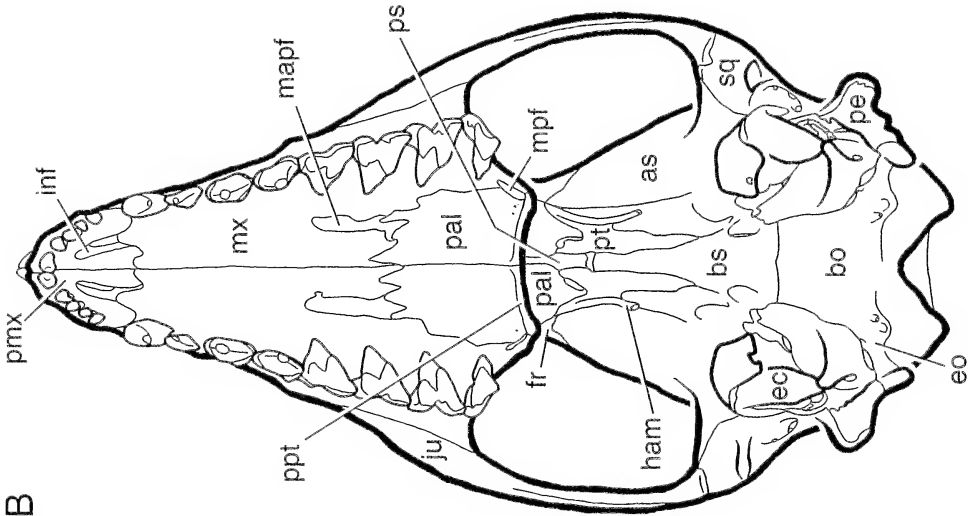
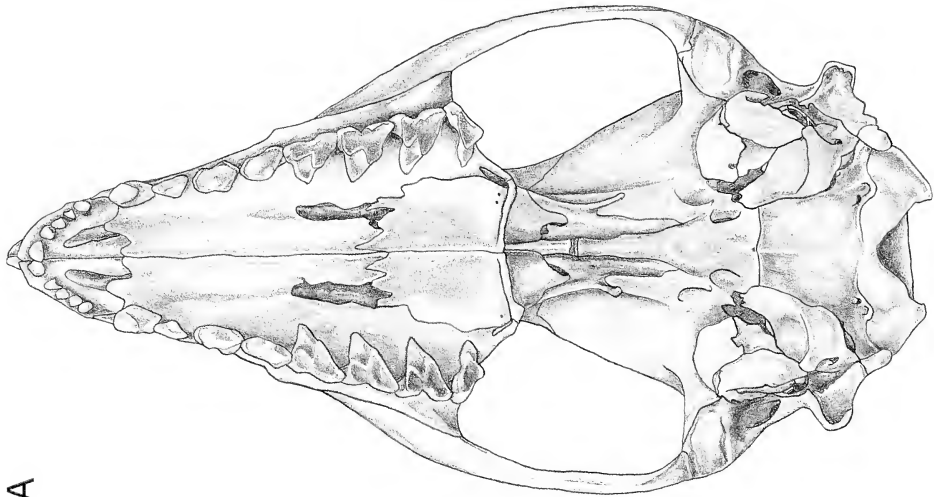
The pterygoid has a minor exposure in the floor of the sphenorbital fissure in the posteroventral aspect of the medial orbit wall (Fig. 4). It is a flat, trapezoidal sliver of bone, longer than wide. It contacts the presphenoid and basisphenoid medially, the alisphenoid posteriorly and laterally, and the palatine anteromedially. Anterolaterally, it is separated from the palatine by an irregular opening. The anterior opening of the pterygoid canal, which is within the sphenorbital fissure and not visible in lateral view, lies between the posterolateral aspect of this lamina of pterygoid and the overlapping alisphenoid. The alisphenoid bears a notch that forms the posterior and lateral borders of this aperture. Extending anteriorly a short distance from the notch is a narrow groove on the pterygoid for the contents of the pterygoid canal.

Vomer

The vomer is not visible in any of the illustrated views. According to Macrini (2000), the vomer is a thin, anteroposteriorly elongate bone that contributes to the anterior portion of the nasal cavity. It articulates with the presphenoid posteriorly, the palatal processes of the maxillae anterodorsally, and the medial palatine processes (vomerine processes) of the premaxillae anteriorly.

Sphenoid Complex

Clark and Smith (1993) identify four bones in the sphenoid complex of *Monodelphis domestica*. The presphenoid and basisphenoid are midline elements in the skull base between the choanae and ear region. Attached to the presphenoid are the paired



orbitosphenoids, which have a small exposure in the medial orbital wall. Attached to the basisphenoid are the paired alisphenoids, which have a much more substantial contribution to the medial wall of the orbitotemporal fossa. According to Clark and Smith (1993), the presphenoid and orbitosphenoids arise on postnatal day 13 and 14 from three centers of ossification that fuse to form a T-shaped structure by postnatal day 16. I describe the presphenoid as the midline rod and the orbitosphenoids as the arms of the T. The basisphenoid arises from a single center of ossification on postnatal day 5. Each alisphenoid arises from two centers of ossification on postnatal day 4, one between the ophthalmic (V_1) and maxillary (V_2) divisions of the trigeminal nerve, and the other between the maxillary and mandibular (V_3) divisions of the trigeminal nerve; these two centers fuse medial to the foramen rotundum by postnatal day 7 (cf. Maier, 1987a). The basisphenoid and alisphenoid are fused together by postnatal day 25. The landmarks that I employ to demarcate the basisphenoid and alisphenoid in the adult skull are the foramen rotundum, which ontogenetically is entirely within the alisphenoid (Clark and Smith, 1993), and the transverse canal and carotid foramina, which ontogenetically are entirely within the basisphenoid (Wible, unpubl. observ.; Sánchez-Villagra, pers. commun.).

Presphenoid

In ventral view (Fig. 5), the unpaired presphenoid is a rod-shaped element in the midline roof of the nasopharyngeal passage that extends and tapers anteriorly deep into the nasal cavity, where it contributes to the nasal septum, there being no independent ethmoid ossification in marsupials (Broom, 1926). Laterally, within the nasopharyngeal passage, the presphenoid contacts, from anterior to posterior, the palatine and pterygoid; and posteriorly, it contacts the basisphenoid.

In lateral view (Fig. 4), a small quadrangular exposure of the posterodorsal presphenoid is visible in the depths of the sphenorbital fissure, where it contributes to the anteroventral floor. It has sutural contact with the palatine and pterygoid laterally, and the basisphenoid posteriorly. Anterodorsally, it is merged with the left and right orbitosphenoid.

Orbitosphenoid

The paired orbitosphenoid has a small exposure in the medial orbital wall, anterior to the sphenorbital fissure (Fig. 4). In lateral view, the orbitosphenoid is roughly wedge-shaped. It is situated anterodorsal to and is continuous with the presphenoid. For descriptive purposes, the orbitosphenoid can be treated as having anteroventral and posterodorsal parts, with the wedge angled such that the anteroventral part is medial to the posterodorsal one. The anteroventral part contacts the palatine ventrally at a longitudinal suture and the frontal anteriorly at a vertical suture. The posterodorsal part looks somewhat like the front half of a horse with the nose pointing posteriorly. The mane is in contact with the frontal, and the head, neck, and forelimb in contact with the alisphenoid. The anteroventral and posterodorsal parts contribute to the walls of two major apertures: the ethmoidal foramen and sphenorbital fissure. The ventrally directed ethmoidal foramen lies in the suture between the frontal and orbitosphenoid, with the anteroventral part of the orbitosphenoid

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Fig. 5.—*Monodelphis brevicaudata* CM 52729, skull in ventral view excluding mandibles (A) with accompanying line drawing (B). Abbreviations: **as**, alisphenoid; **bo**, basioccipital; **bs**, basisphenoid; **ec**, ectotympanic; **eo**, exoccipital; **fr**, frontal; **ham**, pterygoid hamulus; **inf**, incisive foramen; **ju**, jugal; **mapf**, major palatine foramen; **mpf**, minor palatine foramen; **mx**, maxilla; **pal**, palatine; **pe**, petrosal; **pmx**, premaxilla; **ppt**, postpalatine torus; **ps**, presphenoid; **pt**, pterygoid; **sq**, squamosal.

forming the medial wall and the posterodorsal part the posterior and posterolateral walls. Running ventrally from the posterior half of the ethmoidal foramen onto the anteroventral part of the orbitosphenoid is a distinct sulcus that curves posteriorly. The large, ovoid, anterolaterally directed sphenorbital fissure has walls made by the orbitosphenoid, alisphenoid, pterygoid, palatine, and presphenoid. The anteroventral part of the orbitosphenoid forms the anterior wall and the posterodorsal part the anterodorsal wall. As is usual in metatherians (Rougier et al., 1998), *Monodelphis* lacks a separate optic foramen for the optic nerve in the orbitosphenoid.

Basisphenoid

The unpaired basisphenoid bone occupies the midline of the basicranium between the presphenoid anteriorly and the basioccipital posteriorly (Fig. 5). It also has a minor exposure laterally deep within the sphenorbital fissure (Fig. 4). The basisphenoid is fused seamlessly with the paired alisphenoids laterally (Fig. 5). Most of what I interpret as the boundary between the basisphenoid and alisphenoid is hidden in ventral view by the underlying pterygoid bone. Posterior to the pterygoid bone, the posterolateral extent of the basisphenoid is marked by the transverse canal and carotid foramina (Fig. 6), which form ontogenetically within the basisphenoid (Wible, unpubl. observ.; Sánchez-Villagra, pers. commun.).

In ventral view (Fig. 5), roughly the anterior half of the exposed basisphenoid is a narrow, gently rounded shaft of bone that lies in the roof of the nasopharyngeal passage between the left and right pterygoids and tapers anteriorly to its suture with the presphenoid. Near the posterior extent of the pterygoids, the basisphenoid widens to encompass two sets of paired foramina (Fig. 6). The more anterolateral set is the transverse canal foramina, the apertures of which are very flattened, almost cigar-shaped, and directed posterolaterally. There is a broad, shallow depression posterolateral to the transverse canal foramen, which likely accommodated the contents of the foramen. The more posteromedial set is the carotid foramina, the apertures of which are ovoid and directed posterolaterally and slightly ventrally. A well-defined, short vascular sulcus on the basisphenoid leads into each carotid foramen from behind. This sulcus is directed toward and in contact with the flat, expanded anteromedial flange of the petrosal (see below). Extending anteriorly from the carotid foramen to the posterior extent of the pterygoid is a raised, rounded ridge. The surface of the basisphenoid between these paired ridges is flat. Running along the lateral aspect of each ridge is a narrow sulcus that ends at a tiny, slit-like foramen between the posterolateral border of the pterygoid and the overlying basisphenoid. This narrow aperture is the posterior opening into the pterygoid canal. The surface of the basisphenoid posteromedial to the carotid foramina is flat, but off the midline is subtly rugous and projects slightly ventrally at its contact with a surface with similar characteristics on the basioccipital. This surface on the basisphenoid-basioccipital suture likely is for the attachment of the longus capitis muscle, based on the dog (Evans, 1993).

In lateral view (Fig. 4), the anterodorsal surface of the basisphenoid is visible in the floor of the sphenorbital fissure. Its shape mirrors that of the ventral surface; that is, it is a rounded shaft. It contacts the presphenoid anteriorly and the pterygoid laterally.

Alisphenoid

The paired alisphenoid bones are situated on either side of the basisphenoid and contribute to the side wall of the braincase, the skull base in front of the ear region, and the auditory bulla (Figs. 5–6). The alisphenoids are fused seamlessly with the basisphenoid. As

stated above, most of the boundary between the alisphenoids and basisphenoid is hidden in ventral view by the underlying pterygoid bones. The medial limit of the alisphenoid lies medial to the foramen ovale and the foramen rotundum, which ontogenetically form in association with the alisphenoid (Maier, 1987a; Clark and Smith, 1993).

In lateral view (Fig. 4), the alisphenoid is roughly pentagonal to which are added two narrow processes, at the anteroventral and posteroventral margins, respectively. The five sides of the pentagon are as follows: anteroventrally, the sphenorbital fissure and the suture with the orbitosphenoid; anterodorsally, the suture with the frontal; posterodorsally, the suture with the parietal; posteroventrally, the suture with the squamosal; and ventrally, the skull margin. A distinct infratemporal crest divides the lateral surface of the pentagon into an inferior one-third facing ventrolaterally into the infratemporal fossa and a superior two-thirds facing laterally into the temporal fossa. This crest marks the ventral limit of the attachment of the temporalis muscle, based on *Didelphis marsupialis* (Turnbull, 1970). Extending anteroventrolaterally from the anteroventral margin of the pentagon is the anterior process of the alisphenoid. This long, straight splint of bone tapers to a point dorsal to the minor palatine foramen. It contacts the basisphenoid, pterygoid, and palatine dorsally, and the pterygoid, palatine, and maxilla ventrally. At the root of the anterior process are the circular, anteriorly directed foramen rotundum (most of which is hidden in lateral view) and, anteromedial to that, the much larger sphenorbital fissure. The alisphenoid entirely encloses the foramen rotundum, but encloses only the posterolateral half of the sphenorbital fissure. Extending ventrally from the posteroventral margin of the pentagon is the alisphenoid tympanic process, which curves posteriorly, cupping the ectotympanic bone and forming the anterior wall of the auditory bulla. Anterior to the base of the alisphenoid tympanic process is the foramen ovale. In the interval between the foramen rotundum anteriorly and the foramen ovale posteriorly, the alisphenoid is gently rounded.

The bulk of the alisphenoid visible in ventral view lies within the infratemporal fossa (Fig. 5). Posterolaterally, the alisphenoid has a triangular glenoid process in contact with the squamosal that provides the anteromedial articular surface of the temporomandibular joint (Fig. 6). Posteromedial to the glenoid process is the inflated, bowl-shaped tympanic process of the alisphenoid (Fig. 6). The posterolateral border of the tympanic process abuts the ectotympanic and anterior process of the malleus; the posteromedial border has a distinct notch that marks the passage of the auditory or eustachian tube. In the posteroventral margin of the tympanic process is a small opening of unknown function on the left side of CM 52729 that is a notch on the right side. Lateral to this notch on the right side, opposite the ventral end of the anterior process of the malleus is a faint notch leading to a short sulcus on the extratympanic surface of the tympanic process. The left side has no notch or sulcus, but only a gap, which is indicated in Figure 6 ("glf"). In other specimens (e.g., *Monodelphis domestica* CM 80016), this notch is closed to a foramen. I interpret this gap, notch, and foramen as for the chorda tympani nerve, a branch of the facial nerve that exits the middle ear and enters the infratemporal fossa. The gap, notch, or foramen for the chorda tympani is a glaserian fissure, which in placentals typically lies near the juncture of the petrosal, ectotympanic, squamosal, and alisphenoid (Klaauw, 1931). The concave inner surface of the alisphenoid tympanic process in CM 52729, which walls an extensive alisphenoid hypotympanic sinus, is expanded posteriorly to contact the petrosal anterodorsal to the tuberculum tympani. Medial to the tympanic process is the elongate foramen ovale, which lies between the alisphenoid and petrosal (Fig. 6). Leaving the anterior end of the foramen ovale and directed ventrolaterally is a sulcus, partly on the skull base and partly on the tympanic process. The foramen ovale is continuous medially with a small aperture between the basisphenoid and petrosal. The walls of this aperture are

rounded, and it transmitted the greater petrosal nerve from the hiatus Fallopii to the pterygoid canal (Wible, unpubl. observ.).

A small area of alisphenoid in the temporal fossa lateral to the parietal and squamosal is visible in dorsal view (Fig. 1). Noteworthy is the alisphenoid's contribution to the dorsal surface of the posterior zygomatic root, which served as attachment area for the temporalis muscle, based on *Didelphis marsupialis* (Turnbull, 1970).

Squamosal

The paired squamosal bones have a flattened squamous portion in the posteroventral side wall of the braincase, a zygomatic process contributing to the posterior half of the zygoma, and the glenoid fossa, the skull's component of the temporomandibular joint (Figs. 1, 2, 4–6).

In lateral view (Fig. 2), the squama of the squamosal is somewhat quadrangular in shape. Because of the thinness of the braincase bones, it is apparent that the bulk of the squama does not contribute to the primary side wall per se; it overlies the parietal anterodorsally, the alisphenoid anteriorly, and the petrosal posteriorly. There is only a narrow area dorsal to the level of the postglenoid process where the squama is the primary wall. Anteriorly, the squama contacts the alisphenoid. Its dorsal border has a gently sinuous contact with the parietal, and the posterodorsal corner has a narrow contact with the interparietal. The posterior border of the squama contacts the mastoid exposure of the petrosal at a suture that contains the posttemporal notch, and forms the ventral one-third of the nuchal crest (Fig. 9). The posteroventral corner of the squama is prolonged ventrally into a stout posttympanic process (Fig. 2), which is buttressed medially by the mastoid process of the petrosal (Fig. 9). The ventral border of the squama is concave between the postglenoid and posttympanic processes, and this area is occupied by the external acoustic meatus. Anterodorsal to the posttympanic process is a large, posterolaterally directed suprameatal foramen (Fig. 4), which connects through the squamosal to the postglenoid foramen on the ventral surface (Fig. 6). Posterior to the suprameatal foramen is a wide depression, which dorsally includes a short, posterodorsally directed sulcus (Fig. 2).

In lateral view (Fig. 2), the zygomatic process of the squamosal lies in the posterior half of the zygoma and is underlain by the glenoid process of the jugal. At the posterior root of the zygomatic process is the prominent, ventrally directed postglenoid process. Dorsal to the postglenoid process is a small, anterolaterally directed, unnamed opening (Fig. 4). Based on CM 76731, I confirm that this opening communicates through the squamosal with the postglenoid foramen on the ventral surface. In dorsal view (Fig. 1), the dorsal edge of the zygoma has a ridge that extends from the frontal process of the jugal to where the posterior root of the zygoma merges with the braincase. Anteriorly, this ridge is very sharp; posteriorly, it is rounded and forms the posterior wall of a triangular depression on the dorsum of the posterior root of the zygoma. The anteromedial portion of this depression is formed by the alisphenoid, the remainder by the squamosal. This depression provides attachment for the temporalis muscle, based on *Didelphis marsupialis* (Turnbull, 1970). In the posterior corner of this depression is a small foramen in the squamosal that is hidden in dorsal view by the ridge running along the dorsal edge of the zygoma. This foramen communicates with the postglenoid foramen.

The most conspicuous features on the squamosal in ventral view are the glenoid fossa at the posterior root of the zygoma and behind that, the postglenoid process and foramen (Fig. 6). The glenoid fossa is ovoid, wider than long, and with the exception of the narrow articular surfaces on the glenoid processes of the jugal and alisphenoid is entirely on

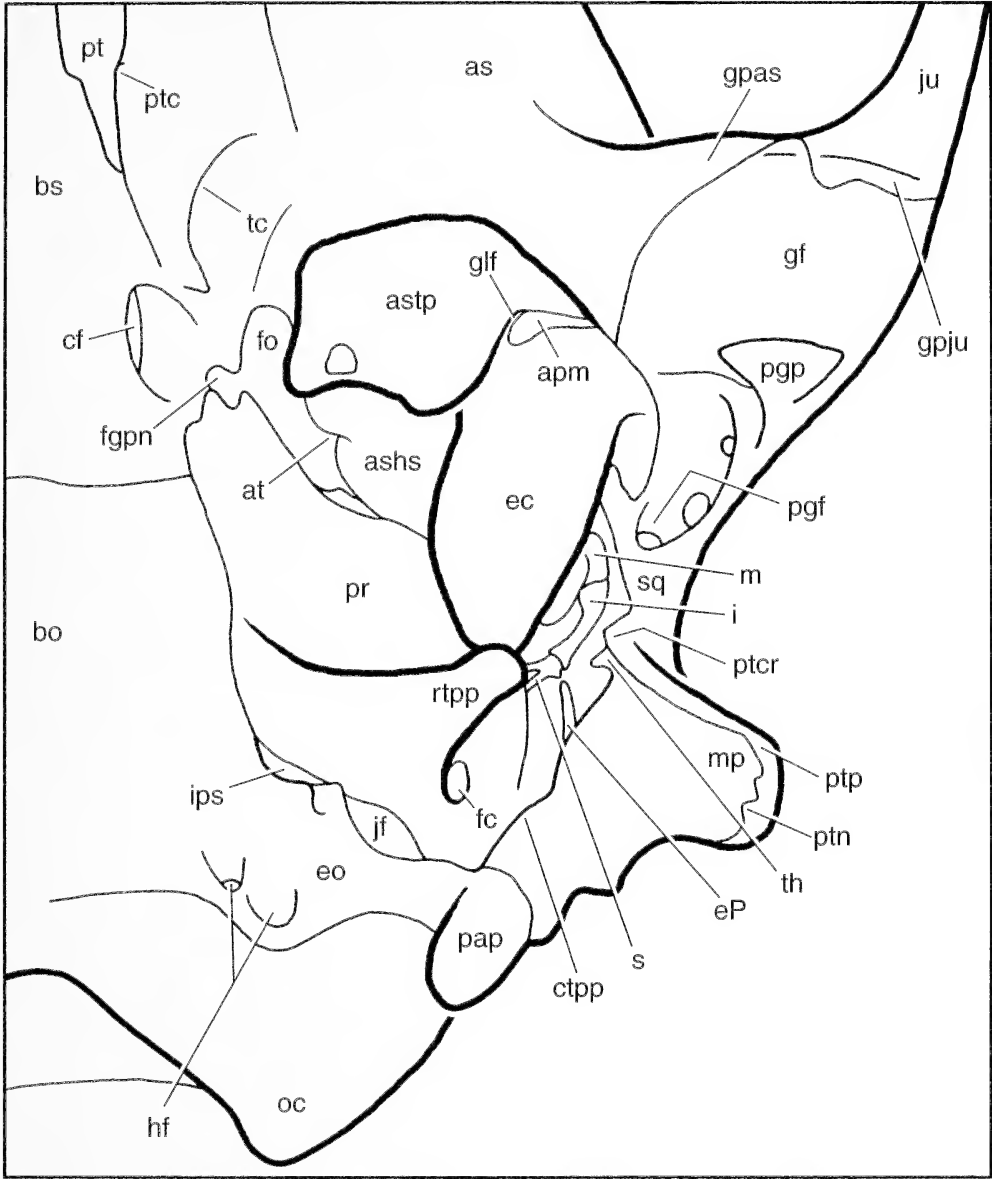


Fig. 6.—*Monodelphis brevicaudata* CM 52729, line drawing of left ear region in ventral view. Abbreviations: **apm**, anterior process of the malleus; **as**, alisphenoid; **ashs**, alisphenoid hypotympanic sinus; **astp**, alisphenoid tympanic process; **at**, groove for the auditory tube; **bo**, basioccipital; **bs**, basisphenoid; **cf**, carotid foramen; **ctpp**, caudal tympanic process of the petrosal; **ec**, ectotympanic; **eo**, exoccipital; **eP**, element of Paaw; **fc**, fenestra cochleae; **fgpn**, foramen for greater petrosal nerve; **fo**, foramen ovale; **gf**, glenoid fossa; **glf**, glaserian fissure; **gpas**, glenoid process of the alisphenoid; **gpju**, glenoid process of the jugal; **hf**, hypoglossal foramen; **i**, incus; **ips**, foramen for the inferior petrosal sinus; **jf**, jugular foramen; **ju**, jugal; **m**, malleus; **mp**, mastoid process; **oc**, occipital condyle; **pap**, paracondylar process of the exoccipital; **pgf**, postglenoid foramen; **pgp**, postglenoid process; **pr**, promontorium; **pt**, pterygoid; **ptc**, pterygoid canal; **ptcr**, posttympanic crest; **ptn**, posttemporal notch; **ptp**, posttympanic process; **rtp**, rostral tympanic process of the petrosal; **s**, stapes; **sq**, squamosal; **tc**, transverse sinus canal; **th**, tympanohyal.

the squamosal. The fossa is also entirely on the posterior zygomatic root and not on the braincase proper. Forming the posteromedial wall of the glenoid fossa is the stout postglenoid process, which in occipital view is U-shaped with the lateral arm of the U more erect than the medial. The ventral limit of the process, the bottom of the U, is asymmetrical in ventral view, with the medial half thinner and the lateral half more bulbous posteriorly.

Posteromedial to the postglenoid process is the large, ovoid postglenoid foramen (Fig. 6). This aperture is entirely within the squamosal; however, underlying the squamosal along the foramen's medial edge is the anterior crus of the ectotympanic. In ventral view, three openings increasing in size posteriorly are visible within the substance of the postglenoid foramen. By far the largest, the posterior opening curves posterodorsally into the squamosal. It represents the true intramural continuation of the postglenoid foramen (that is, the conduit for the sphenoparietal emissary vein), which communicates with the suprameatal foramen on the side wall of the braincase described above. The anterior two openings (postzygomatic foramina of Gregory, 1910) are in the anterior wall of the main postglenoid channel; they are directed anterodorsally into the squamosal (with the anterior one communicating with the small unnamed foramen described above on the posterior zygomatic root dorsal to the postglenoid process, based on CM 76731). The anterior foramen is round and the middle one is ovoid.

Posterior to the postglenoid foramen, the squamosal narrows considerably and then expands chiefly posterolaterally to form the posttympanic process (Fig. 6). The ventral surface of the squamosal between the postglenoid foramen and posttympanic process is dominated by two distinct ridges that meet at roughly 90° to each other. The point at which these ridges meet is a very prominent, sharp, V-shaped process that points ventromedially and overhangs the tympanohyal on the petrosal bone. Wible et al. (in press) called a similar, but more medially expanded version of this process in the Late Cretaceous eutherian *Zalambdalestes* the posttympanic crest, a term that I adopt here. The ridge extending anterolaterally from the posttympanic crest is gently concave and forms the dorsal rim of the external acoustic meatus. The ridge extending posterolaterally from the posttympanic crest is straighter, is buttressed by the mastoid process posteriorly, and connects to the posttympanic process.

Petrosal

The paired petrosal bones enclose the organs of hearing and equilibration, provide attachment for the muscles and ligaments of the middle-ear ossicles, and include grooves, canals, and foramina for components of the cranial vascular and nervous systems. Two divisions of the petrosal are generally recognized: the pars cochlearis, housing the cochlear duct and saccule of the inner ear, and the pars canalicularis, housing the utricle and semicircular canals. Because the petrosal has played a prominent role in metatherian phylogenetics (e.g., Archer, 1976; Wible, 1990; Rougier et al., 1998; Sánchez-Villagra and Wible, 2002), detailed descriptions of the various surfaces of the petrosal of *Monodelphis* are included here, based on an isolated left petrosal of *Monodelphis* sp. CM 5024 (which I provisionally identify as *M. domestica*) and an isolated right petrosal of *M. breviceaudata* CM 5061. The former is illustrated in three views in Figures 7–8 (tympanic, dorsal, and lateral) and is the principal basis for the following descriptions, with differences between CM 5024 and 5061 noted. Information on the middle-ear ossicles and neighboring bones is taken from *M. breviceaudata* CM 52729, which is illustrated in ventral and occipital views in Figures 6 and 9. Following the descriptions of the three illustrated views of the isolated petrosal is a section on the principal veins of the petrosal bone.

Tympanic View.—The two divisions of the petrosal are most readily seen in the tympanic or ventral view (Fig. 7A, D); the pars cochlearis is represented by the promontorium and

the flange projecting anteromedially from it, and the pars canalicularis by the bone lateral and posterior to the promontorium. The bulbous shape of the promontorium reflects the enclosed coiled cochlear duct, which in adult *Didelphis virginiana* has two and one-fourth turns (Larsell et al., 1935). There are two openings in the outer contour of the promontorium: posterolaterally, the fenestra vestibuli, and posteriorly, the fenestra cochleae. The slightly oval-shaped fenestra vestibuli, which houses the footplate of the stapes, has a stapedia ratio (of Segall, 1970, length/width) of 1.45 in CM 5024 (it was not possible to measure CM 5061, because the footplate of the stapes partially obscures the posterior dimension of the fenestra vestibuli). Other didelphids measured by Segall (1970) are comparable (*Metachirus* and *Didelphis*, 1.3; *Marmosa*, 1.4; *Caluromys* and *Philander*, 1.5). The fenestra vestibuli is not fully visible in the direct ventral view (Fig. 6); it is directed laterally and slightly ventrally, and sits in a shallow vestibular fossula, recessed from the surrounding bone. The more elliptical fenestra cochleae, covered in life by the secondary tympanic membrane, is also not fully visible in ventral view, because its ventromedial aspect is hidden by the back of the rostral tympanic process of the petrosal (see below; Fig. 6). It is this hidden portion of the fenestra cochleae that has a shallow cochlear fossula.

The most noteworthy feature on the promontorium is the rostral tympanic process of the petrosal (rtpp) (Fig. 7A, D). This finger-like process projects ventroanterolaterally from the posteromedial surface of the promontorium and abuts the posterior crus of the ectotympanic (Fig. 6). Extending anteromedially and posterolaterally from the main finger-like process are low ridges (Figs. 6, 7A, D). The anteromedial ridge extends the length of the promontorium and contacts the basioccipital bone, distal to the basioccipital-basisphenoid suture (Fig. 6). The shorter posteromedial ridge forms the dorsomedial lip of the cochlear fossula and fenestra cochleae (Figs. 6, 7A, D).

Projecting anteromedially from the promontorium is a fairly flat shelf of bone, the anteromedial flange, which narrows slightly anteriorly and is directed toward the carotid sulcus and foramen within the basisphenoid (Fig. 6). Although the flange has no sign of a vascular sulcus, the internal carotid artery may have contacted this surface en route to the basisphenoid bone. The medial side of the flange contacted the basioccipital and basisphenoid, and the lateral side formed the posteromedial border for the large foramen ovale. The lateral edge of the flange has a narrow, shallow surface that probably accommodated (or provided attachment area for) the tensor tympani muscle (Fig. 7A, D).

As stated above, the pars canalicularis is represented by the bone projecting from the lateral and posterior aspects of the promontorium (Fig. 7A, D). On the pars canalicularis are two ridges at roughly right angles to one another that meet at the posterolateral corner of the petrosal. At their juncture is a stout, posterolaterally directed mastoid process, which is covered anterolaterally by the posttympanic process of the squamosal (Fig. 6). The ridge running posteromedially from the mastoid process is the caudal tympanic process of the petrosal (ctpp) (Fig. 7A, D). The cttp in the isolated petrosals (CM 5024 and 5061) decreases in height medially, but this is not the case in the skull (CM 52729). The medial end of the cttp abuts the paracondylar process of the exoccipital bone (Fig. 6). The ridge that runs anteriorly from the mastoid process is the crista parotica (Fig. 7A, D), which in the skull is hidden by the squamosal bone (Fig. 6). The crista parotica is much shorter and thinner than the cttp; it extends to approximately the level of the anterior edge of the fenestra vestibuli. At the posterior end of the crista parotica is a thickening, the ventral end of which has a flat triangular surface facing ventromedially. The thickening is the tympanohyal and the triangular surface is the contact for the stylohyal (not preserved). Posterior to the tympanohyal is the stylomastoid notch by which the facial nerve left the middle ear.

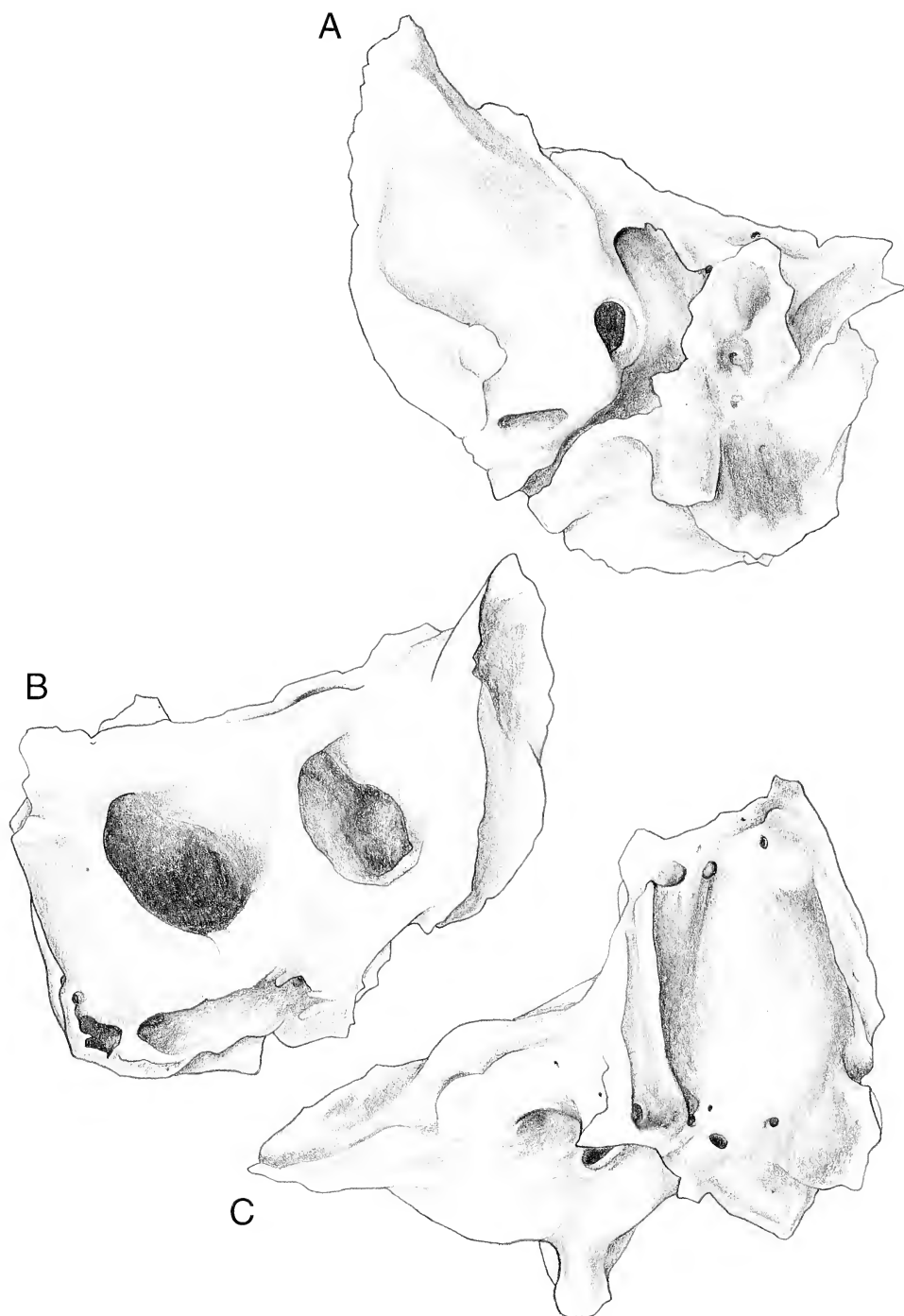


Fig. 7.—*Monodelphis* sp. CM 5024, left petrosal in ventral view (A), dorsal view (B), and lateral view (C), with accompanying line drawing (D), (E), and (F), respectively. Abbreviations: **amf**, anteromedial flange; **av**, aqueductus vestibuli; **br**, broken; **cc**, cochlear canaliculus; **cp**, crista parotica; **cr**, crista petrosa; **crc**, crus commune; **ctpp**, caudal tympanic process of the petrosal; **er**, epitympanic recess; **fai**, foramen acousticum inferius; **fas**, foramen

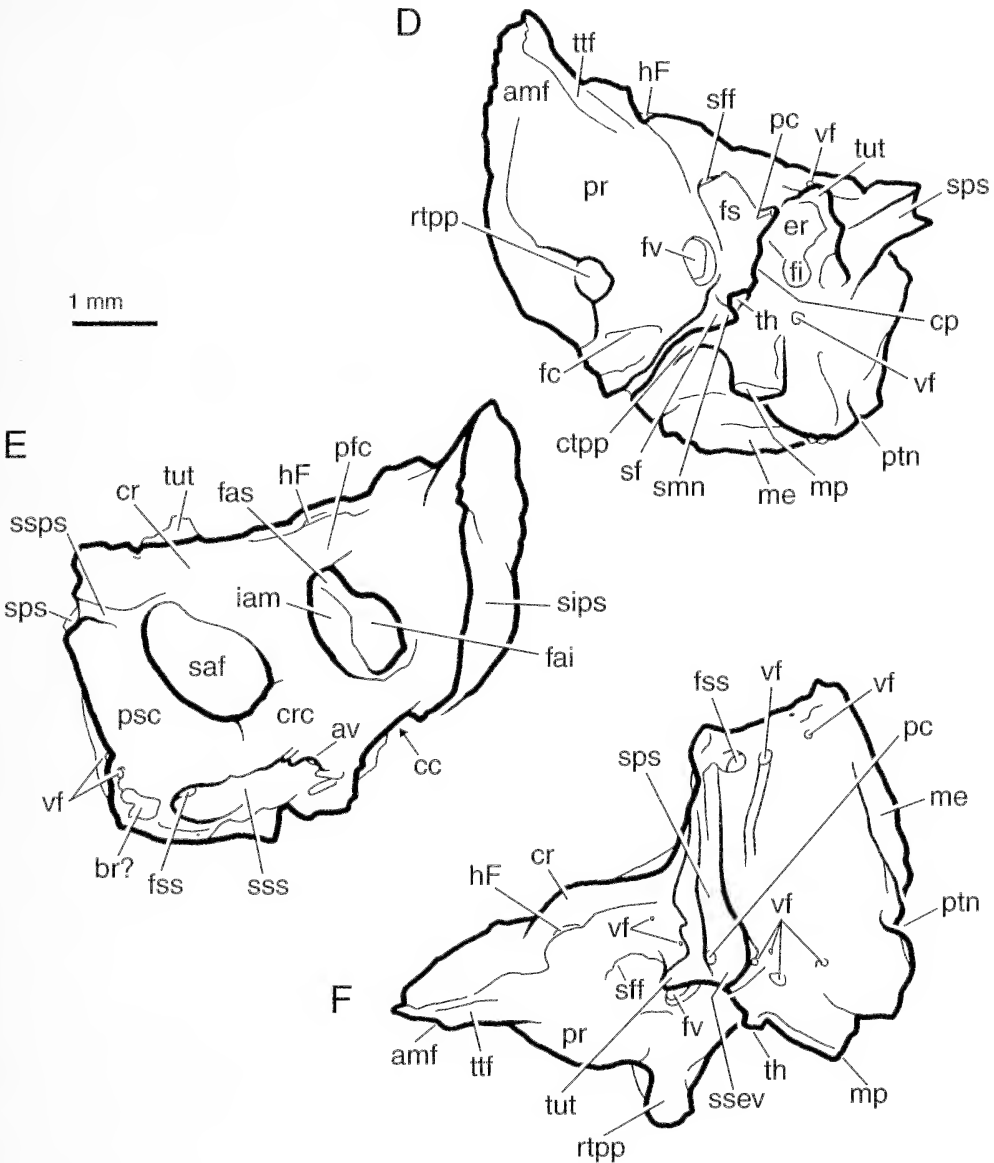


Fig. 7.—Continued.

acusticum superius; **fc**, fenestra cochleae; **fi**, fossa incudis; **fss**, foramen for the sigmoid sinus; **fv**, fenestra vestibuli; **hF**, hiatus Fallopii; **iam**, internal acoustic meatus; **me**, mastoid exposure; **mp**, mastoid process; **pc**, prootic canal; **pfc**, prefacial commissure; **pr**, promontorium; **psc**, posterior semicircular canal; **ptn**, posttemporal notch; **rtp**, rostral tympanic process of the petrosal; **saf**, subarcuate fossa; **sf**, stapedius fossa; **sff**, secondary facial foramen; **sips**, sulcus for the inferior petrosal sinus; **smn**, stylomastoid notch; **sps**, sulcus for the prootic sinus; **ssev**, sulcus for the sphenoparietal emissary vein; **ssps**, sulcus for the superior petrosal sinus; **sss**, sulcus for the superior petrosal sinus; **th**, tympanohyal; **ttf**, tensor tympani fossa; **tut**, tuberculum tympani; **vf**, vascular foramen.

Between the ctp_p and the rear of the promontorium is a deep depression, the bulk of which is not visible in tympanic view (Figs. 6, 7A, D). The narrower medial part of this depression is the post-promontorial tympanic sinus of Wible (1990); the broader, deeper, oval, lateral part is the fossa for the stapedius muscle. The width of the stapedius fossa is roughly three quarters the length of the ctp_p. Projecting anteroventrally from the stapedius fossa is a thin rod of bone in CM 5024 (not illustrated in Figure 7, because it is displaced), 5061, and 52729 that is attached to the muscular process of the stapes by a ligament in CM 52729 (Fig. 6). This is the ossified element of Paaw, which is the functional equivalent of a sesamoid bone in the tendon of the stapedius muscle. The surface of the pars canalicularis posterolateral to the ctp_p is the mastoid exposure, the surface of the petrosal exposed on the occiput.

Between the crista parotica and the fenestra vestibuli is a broad, shallow, anteriorly directed facial sulcus (Fig. 7A, D), so-called because its principal occupant was the facial nerve. Within the sulcus, lateral to the facial nerve ran the much smaller lateral head vein. Opening posteromedially into the lateral aspect of the facial sulcus at the level of the anterior edge of the fenestra vestibuli is the tympanic aperture of the prootic canal. The prootic canal is the route by which the prootic sinus communicated with the lateral head vein (Wible, 1990; Wible and Hopson, 1995). At the level of the tympanic aperture of the prootic canal, the facial sulcus turns anteromedially and after a short course enters the oval secondary facial foramen. The bone immediately anterior to the secondary facial foramen represents the floor of the cavum supracochleare, the space that housed the geniculate ganglion of the facial nerve (Gaupp, 1908). Anterior to this floor, the anteriormost roof of the hiatus Fallopii is visible. The hiatus Fallopii, not fully visible in any of the three views illustrated, is a gap similar in size to the secondary facial foramen. It transmitted the greater petrosal nerve (palatine ramus of the facial nerve).

Lateral to the facial sulcus is a bony shelf of similar dimensions, but whose surface is very irregular (Fig. 7A, D). The lateral edge of this shelf has a ridge that is hidden in the skull by the squamosal and that ends anteriorly in a sharp, anteroventrally directed process. This process is called the tuberculum tympani, because it resembles the structure so identified by Toeplitz (1920) in pouch young *Didelphis marsupialis*. Following Kuhn and Zeller (1987), this is the homologue of the tegmen tympani of placentals. The shelf medial to the lateral ridge has two depressions. Posteriorly is a smaller, circular, deeper depression, the fossa incudis for the short process (crus breve) of the incus. The fossa incudis is bordered medially by the crista parotica and laterally by the squamosal bone. Anterior to and continuous with the fossa incudis is a broader, shallower depression, the epitympanic recess over the mallear-incudal articulation (Klaauw, 1931). The epitympanic recess is bordered medially by a very low ridge, the anterior continuation of the crista parotica, and laterally by the lateral ridge and squamosal.

Dorsal View.—The dorsal or endocranial view (Fig. 7B, E) is dominated by two large openings, the internal acoustic meatus anteromedially and the subarcuate fossa posterolaterally. The smaller internal acoustic meatus for the vestibulocochlear nerve lies in the roof of the pars cochlearis, and the subarcuate fossa, which accommodated the paraflocculus of the cerebellum, is in the roof of the pars canalicularis. The floor of the internal acoustic meatus has a depression that is roughly dumbbell shaped, with the medial and lateral ends of the dumbbell representing the foramen acusticum inferius and superius, respectively. Constricting the central axis of the dumbbell from in front and behind is the low transverse crest. The larger foramen acusticum inferius is kidney-bean shaped and has some tiny perforations that are interpreted as evidence of the spiral cribriform tract (tractus spiralis foraminosus), which transmitted fascicles of the cochlear nerve. In the posterior part of the foramen acusticum inferius is a shallow pit that may represent the foramen singulare

for passage of some bundles of the vestibular nerve. The foramen acusticum superius, largely hidden in dorsal view, has a smaller anterior opening into a canal for the facial nerve and a posterior blind pit, which is interpreted as the cribriform dorsal vestibular area for passage of the remaining bundles of the vestibular nerve. Posterolateral to the internal acoustic meatus is the larger and deeper subarcuate fossa. Components of the semicircular canal system occupy the bone forming the rim of the aperture into the subarcuate fossa. The posterior semicircular canal forms the posterolateral rim, and the crus commune, the conjoined anterior and posterior semicircular canals, forms the posteromedial rim. The aperture into the subarcuate fossa is constricted posteriorly, that is, within the fossa the paraflocculus was expanded and occupied the space dorsal to the posterior semicircular canal and crus commune.

The medial edge of the pars cochlearis has two distinct surfaces (Fig. 7B, E). Anteriorly is the flat roof of the anteromedial flange, which has an incurved lateral wall that produces a distinct pocket. Based on the CT slices in Macrini (2000), this pocket accommodated the basisphenoid and basioccipital bones. Behind this pocket is a broad sulcus for the inferior petrosal sinus, which originated at the cavernous sinus around the hypophysis and left the skull via its own foramen anterior to the jugular foramen.

Anterior to the internal acoustic meatus and subarcuate fossa is a low crest, the crista petrosa (Fig. 7B, E). The medialmost portion of the crista petrosa, the part anterior to the internal acoustic meatus, is the prefacial commissure, the ossified chondrocranial component of the same name. Anterior to and hidden by the prefacial commissure is a narrow gap directed anteromedially, the hiatus Fallopii. The anterior border of the hiatus is formed by a narrow, low ridge that runs nearly the length of the pars cochlearis.

Three vascular sulci are situated in the vicinity of the subarcuate fossa (Fig. 7B, E). At the posterolateral corner of the petrosal is a sulcus running forward toward the crista petrosa along the lateral border of the subarcuate fossa. This short, shallow sulcus for the superior petrosal sinus cannot be traced beyond the anterior rim of the subarcuate fossa. Immediately posterolateral to the sulcus for the superior petrosal sinus is a barely visible sulcus for the prootic sinus, which is described with the lateral view where it is more fully apparent. Posteromedial to the subarcuate fossa, behind the crus commune and posterior semicircular canal, is a well-developed sulcus, the principal occupant of which was the sigmoid sinus. There are foramina at each end of this sulcus. Laterally is an oval aperture directed anterolaterally into a canal, the canal for the sigmoid sinus; medially is the slit-like vestibular aqueduct, which transmitted the endolymphatic duct into the petrosal. CM 5061 differs in that the foramen for the sigmoid sinus is situated more laterally, which creates a longer sulcus for the sigmoid sinus.

Finally, immediately posteroventral to and hidden by the bony bar behind the foramen acusticum inferius is another narrow, slit-like opening, the cochlear canaliculus, which transmitted the perilymphatic duct into the petrosal (Fig. 7B, E).

Lateral View.—The two divisions of the petrosal are also visible in the lateral or squamosal view. In Figure 7C and F, the pars canicularis lies posterior to and includes the sulcus for the prootic sinus and the tuberculum tympani; the pars cochlearis lies anterior and ventral to these structures. As in the ventral view, the pars cochlearis in lateral view is dominated by the promontorium and two projections from it: ventrally, the rtp, and anteriorly, the anteromedial flange. The lateral edge of the anteromedial flange has a narrow depression that is interpreted as the fossa for the tensor tympani muscle. The dorsal edge of the pars cochlearis includes the low crista petrosa. Ventral to the crista petrosa is another low ridge that runs nearly the length of the pars cochlearis (this ridge is significantly lower in CM 5061 than in CM 5024). Posteriorly, this ridge runs somewhat parallel to the crista petrosa; anteriorly, it is positioned more ventrally and forms the dorsal border of the fossa

for the tensor tympani. Near the midpoint of and largely hidden by this ridge is the hiatus Fallopii (in light of the lower ridge in CM 5061, the hiatus Fallopii is more visible in lateral view). More posteriorly, between this ridge and the tuberculum tympani are two tiny vascular foramina that likely drained venous blood from the petrosal (only the posteroinferior foramen is preserved in CM 5061). The petrosals of juvenile *Monodelphis domestica* studied by the author (reported in Rougier et al., 1992) contain a large amount of venous blood with various points of egress. Ventral to these tiny foramina are two larger apertures on the pars cochlearis of CM 5024 partially visible in lateral view, the secondary facial foramen in front and the fenestra vestibuli behind.

The pars canicularis is roughly trapezoidal in lateral view (Fig. 7C, F) with posterior, ventral, anterior, and dorsal sides. In the ventral part of the posterior side is the mastoid process and dorsal to it, one-third the way up the posterior side, is a distinct vascular notch, the posttemporal notch (this notch is less distinct in CM 5061). In the skull, this notch is covered laterally by the squamosal to complete a posttemporal foramen, which in CM 52729 does not have a visible aperture (Fig. 9) and apparently did not transmit any substantial structure. There is no indication in CM 5024 and 5061 of a sulcus running anteriorly from the posttemporal notch in contrast to the condition in some other didelphids (see Wible, 1990:fig. 4B; Sánchez-Villagra and Wible, 2002). Running dorsally and slightly anteriorly from the posttemporal notch in figure 7C is a low ridge that delimits the covered and uncovered portions of the pars canicularis. Posterior to this ridge is the mastoid exposure; anterior to it, the remaining surface of the pars canicularis is covered by the squamosal bone in the skull.

Anterior to the mastoid process, the ventral side of the pars canicularis is formed by the tympanohyal, crista parotica, and tuberculum tympani (Fig. 7C, F). Dorsal to the mastoid process and tympanohyal are four small vascular foramina that likely drained venous blood from the petrosal (only two foramina are present in CM 5061).

The anterior side of the pars canicularis is formed ventrally by the tuberculum tympani, and posterior and dorsal to that by a longitudinal vascular sulcus (Fig. 7C, F). The occupant of this sulcus was a vein, the primary egress of which was the postglenoid foramen in the squamosal bone. The secondary, much smaller egress was the prootic canal, the lateral aperture of which is visible in the ventral portion of the longitudinal sulcus (the lateral aperture in CM 5061 is twice the size of that in CM 5024). The lateral aperture of the prootic canal marks the boundary at which the vein occupying the longitudinal sulcus has two different developmental histories (Gelderen, 1924; Wible, 1990; Wible and Hopson, 1995; Rougier and Wible, in press). The portion of the vein above the prootic canal is the retained prootic sinus, one of the first veins draining the brain to appear embryologically; the portion below the prootic canal, the sphenoparietal emissary vein of Gelderen (1924), is a much later addition developmentally. The dorsal side of the pars canicularis is characterized by four vascular foramina. The smallest and most dorsal one leads into the substance of the petrosal; the remaining three lead into a canal for the sigmoid sinus that runs the length of the dorsal side. The anteriormost and largest of these three foramina is directed anterolaterally and transmitted the sigmoid sinus into its canal. The foramen posterior to the foramen for the sigmoid sinus is directed ventrolaterally into a sulcus that extends nearly to the level of the posttemporal notch. The posteriormost and smallest foramen appears to be directed laterally. CM 5061 differs from CM 5024 in that the canal for the sigmoid sinus is very short. Instead of a canal in the petrosal, running nearly the length of the lateral surface of the pars canicularis, there is a sulcus for the sigmoid sinus in the comparable location. The sulcus leads to a foramen near the posterodorsal corner of the lateral surface that after a short bony course opens on the endocranial surface. The

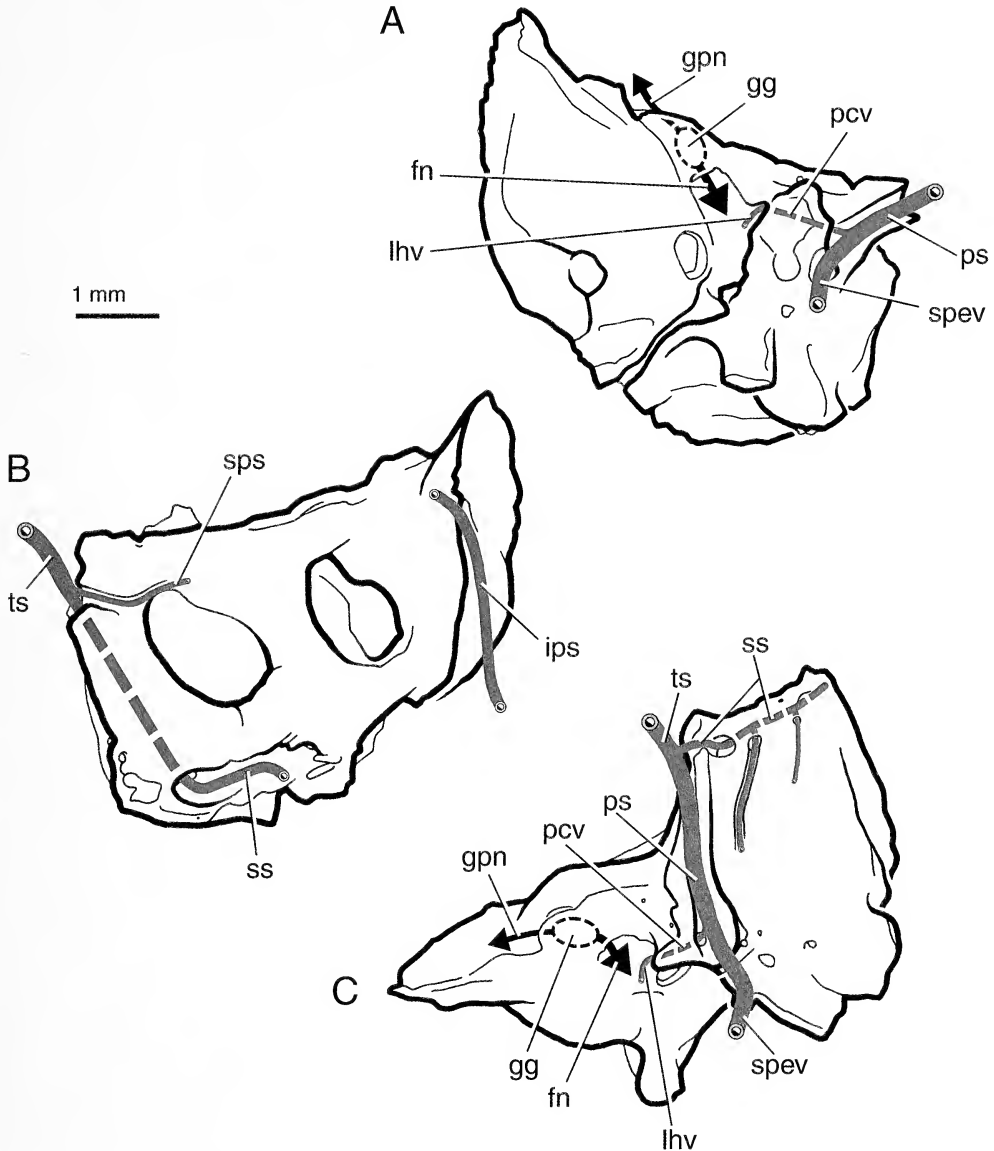


Fig. 8.—*Monodelphis* sp. CM 5024, line drawings of left petrosal with facial nerve and major veins in ventral view (A), dorsal view (B), and lateral view (C). Abbreviations: *fn*, facial nerve; *gg*, geniculate ganglion of the facial nerve; *gpn*, greater petrosal nerve; *ips*, inferior petrosal sinus; *lhv*, lateral head vein; *pcv*, prootic canal vein; *ps*, prootic sinus; *spev*, sphenoparietal emissary vein; *sps*, superior petrosal sinus; *ss*, sigmoid sinus; *ts*, transverse sinus.

sulcus for the sigmoid sinus on the lateral surface in CM 5061 was covered laterally in the skull by the squamosal, thus completing a canal the composition of which differs from that in 5024.

Veins.—As is apparent in the foregoing descriptions, several veins are intimately associated with the petrosal of CM 5024 and 5061. The major foramina, sulci, and canals associated with these veins have been noted above. A comprehensive review of the course

of these veins is included here to document the pathways between the major conduits into and out of the petrosal and skull (Fig. 8). Elsewhere I have published illustrations of the veins of the petrosal in *Didelphis virginiana* (Wible, 1990:fig. 4C, D; Wible and Hopson, 1995:fig. 5). Essentially the same pattern is present in CM 5024 and 5061.

The inferior petrosal sinus runs along the medial edge of the pars cochlearis (Fig. 8B). Anteriorly, the inferior petrosal sinus (sinus petrosus ventralis of Dom et al., 1970) arises from the back of the cavernous sinus, which is situated around the hypophysis above the basisphenoid. The inferior petrosal sinus then runs posteriorly exposed within the floor of the cranial cavity, in the broad sulcus medial to the internal acoustic meatus (Fig. 7B, E). The endocranial position of the inferior petrosal sinus was confirmed in numerous skulls, including CM 52729. This course contrasts with the condition in *Didelphis virginiana*, in which the bulk of the course of the inferior petrosal sinus is not exposed within the cranial cavity, but is within a canal between the petrosal and basioccipital. Just in front of the cochlear canaliculus in *Monodelphis*, the inferior petrosal sinus exits the skull via its own foramen (Fig. 6) and forms the internal jugular vein. Dom et al. (1970) reported that the internal jugular vein in *D. virginiana* is small and drains mainly deep structures of the neck; a similar pattern is likely present in *Monodelphis*.

The other major veins of the petrosal are all distributaries of the transverse sinus. Before addressing the pattern in CM 5024 and 5061, it is instructive to review the pattern in *Didelphis virginiana*, based on Dom et al. (1970), Wible (1990), and Wible and Hopson (1995). According to these authors, the transverse sinus, which runs in the outer edge of the tentorium cerebelli, has three principal distributaries: the superior petrosal sinus (sinus petrosus dorsalis of Dom et al., 1970), the prootic sinus (sinus temporalis of Dom et al., 1970), and the sigmoid sinus. The first distributary is the superior petrosal sinus, which runs forward to the cavernous sinus. An isolated petrosal of *D. virginiana*, CM 23799, shows a well-developed sulcus for the superior petrosal sinus reaching forward to the prefacial commissure. Beyond the origin of the superior petrosal sinus, the transverse sinus divides into the larger prootic sinus and the smaller sigmoid sinus. The prootic sinus runs ventrally in a canal between the petrosal and squamosal and ultimately leaves the skull as the postglenoid vein via the postglenoid foramen in the squamosal. Following Gelderen (1924), Wible (1990) and Wible and Hopson (1995) showed that the vein exiting the postglenoid foramen is composed of two embryologically distinct elements: the ontogenetically older prootic sinus superiorly and the sphenoparietal emissary vein inferiorly. The border between these two is marked by the lateral aperture of the prootic canal, which represents the ontogenetic primary exit of the prootic sinus. The vein within the prootic canal, which connects with the rudimentary lateral head vein, is much reduced in size compared with the prootic sinus and sphenoparietal emissary vein. The remaining distributary of the transverse sinus, the sigmoid sinus, runs medially and then posteriorly, exiting the cranial cavity via the foramen magnum. The isolated petrosal of *D. virginiana* CM 23799 has a deep sulcus for the sigmoid sinus that runs posterior and posteromedial to the posterior semicircular canal and subarcuate fossa.

The isolated petrosals of *Monodelphis* CM 5024 and 5061 by and large conform to the general pattern described above for *Didelphis virginiana*, with bony evidence present for the three distributaries of the transverse sinus. Because the skulls of CM 5024 and 5061 are damaged, it is also possible to document the course of the transverse sinus, which is indicated by a broad sulcus running ventrally and slightly anteriorly from the midline on the endocranial surface of the parietal. This sulcus meets the petrosal posterolateral to the subarcuate fossa, immediately dorsal to the sulcus for the prootic sinus present on the lateral surface of the petrosal (Fig. 8C). From this point of contact, three channels originate. (1) A sulcus for the superior petrosal sinus (Figs. 7B, E, 8B) runs forward along the lateral

contour of the subarcuate fossa in CM 5024 and 5061, differing from that in *D. virginiana* CM 23799 in being weaker and shorter. It is uncertain whether or not this shorter sulcus is truly evidence for a shorter superior petrosal sinus. In contrast to the superior petrosal sinus connecting the transverse and cavernous sinuses reported for *D. virginiana* by Dom et al., (1970), Archer (1976) illustrated the superior petrosal sinus in the dasyurids *Sminthopsis murina* and *Antechinus stuartii* as not extending medial to the level of the internal acoustic meatus and not connecting to the cavernous sinus. (2) The sulcus for the prootic sinus and sphenoparietal emissary vein (Figs. 7C, F, 8C) is essentially identical in *Monodelphis* CM 5024 and 5061 and *D. virginiana* CM 23799, running directly ventrally from the sulcus for the transverse sinus. One difference is that the lateral aperture of the prootic canal is relatively smaller in the latter taxon. (3) The course of the sigmoid sinus (Figs. 7B–C, E–F, 8B–C) exhibits the most pronounced difference among all three isolated petrosals. *D. virginiana* CM 23799 has a sulcus for the sigmoid sinus exposed endocranially, running posterior and posteromedial to the posterior semicircular canal. This is the primitive therian, mammalian, and mammaliaform condition (Kermack et al., 1981; Wible, 1990; Wible et al., 1995, 2001). *Monodelphis* CM 5024 and 5061 differ in that the proximal part of the sigmoid sinus is not exposed endocranially but is enclosed within a canal. The composition and length of the canal differs between CM 5024 and 5061. In the former, the canal is entirely within the petrosal and is longer; in the latter, the canal is between the petrosal and squamosal.

Ectotympanic and Middle-Ear Ossicles

Detailed descriptions of the paired ectotympanic bones and middle-ear ossicles of *Monodelphis* are not included here. The reader is referred to the accounts of *Didelphis virginiana* in Doran (1878), *D. perinigra* in Segall (1969), and *Metachirus* sp. in Fleischer (1973). Photographs of the malleus, incus, and stapes of *M. domestica* are included in Sánchez-Villagra et al. (2002:fig. 10A).

For the sake of completeness, I describe the aspects of the ectotympanic shown in the ventral view (Fig. 6), which exposes most of the outer surface of this irregular U-shaped bone. The anterior leg or crus of the ectotympanic is narrow and has a broad contact with the squamosal, medial to the postglenoid foramen. Anteroventral to the squamosal, the anterior crus has a narrow contact with the alisphenoid tympanic process. At the ventral base of the anterior crus, the anterior surface of the ectotympanic is covered by the anterior process of the malleus, which also contacts the alisphenoid tympanic process. Posterior to the alisphenoid tympanic process, the posterior leg or crus of the ectotympanic is broadened and abuts the rostral tympanic process of the petrosal distally. The sulcus tympanicus, the groove channeling the inner circumference of the ectotympanic to which the tympanum attaches, lies on the extreme medial edge of the bone. Therefore, the expansion of the posterior crus is lateral to the tympanum attachment and contributes to a floor for the external acoustic meatus.

A comment about the stapes is needed in that there is a discrepancy in the literature concerning the presence of an intracural foramen. The photograph of the stapes of *Monodelphis domestica* in Sánchez-Villagra et al. (2002:fig. 10A) shows a well-developed intracural foramen, whereas Archer (1976) reported that the stapes is imperforate in *M. dimidiata* WAM M6785. I checked this feature in the CM *Monodelphis* sample. A perforate stapes as illustrated by Sánchez-Villagra et al. (2002:fig. 10a) occurs in the 14 *M. brevicaudata* and 27 *M. domestica* preserving the bone. In contrast, the stapes is imperforate in the one *M. osgoodi* (5248) preserving the bone and in two *M. dimidiata* (86608, 86609); there is a microperforation in the third *M. dimidiata* (86611) with a stapes.

Occipital Complex

CM 52729 has a single occipital bone that forms the skull base between the ear regions, encircles the foramen magnum, and forms the bulk of the occiput. Developmentally (Clark and Smith, 1993), the occipital is a composite of four bones: unpaired basioccipital and supraoccipital, and the paired exoccipitals. CM 52729 has a remnant of the exoccipital-supraoccipital suture (Fig. 9). However, one juvenile *Monodelphis brevicaudata* (CM 68360) and several juvenile *M. domestica* (CM 80019, 80020, and 80033) preserve sutures delimiting all four bones. Based on these specimens, I describe the basioccipital, exoccipitals, and supraoccipital as separate elements in CM 52729.

Basioccipital

The basioccipital forms the skull base between the petrosals and the anteroventral border of the foramen magnum (Figs. 5–6). It is roughly hexagonal with five straight sides (anterior and paired anterolateral and posterolateral) and a posterior sixth side that is indented by the intercondyloid or odontoid notch (Fig. 5). The anterior side is the horizontal suture with the basisphenoid, which lies at the level of the anterior pole of the petrosal promontorium. The anterolateral side abuts the petrosal promontorium except at its posterior end where there is a gap between the petrosal, basioccipital, and exoccipital for the passage of the inferior petrosal sinus (Fig. 6). The posterolateral side is the fused suture with the exoccipital, which ends posteriorly just lateral to the odontoid notch. The anterior and anterolateral sides project somewhat ventrally. The posterior side is also raised as it bears the medial portion of the left and right occipital condyles, which meet on the midline. Also on the midline of the basioccipital is a raised crest in the form of an inverted Y, which form the medial border of paired oval muscular depressions. Based on the dog (Evans, 1993), these depressions housed the rectus capitis ventralis muscle.

Exoccipital

The paired exoccipitals have two subequal, quadrangular parts: a horizontal one on the skull base (Figs. 5–6) and a vertical one on the occiput (Fig. 9).

In ventral view (Fig. 6), the bulk of the horizontal part bears the occipital condyle, which can be described as two continuous articular surfaces. The smaller anteromedial surface is somewhat teardrop-shaped, with the pointed end on the basioccipital meeting its fellow of the opposite side. The larger posterolateral surface is saddle-shaped and extends onto the occiput. At the posterolateral corner of the horizontal part is a strong, posteroventromedially directed paracondylar process, from which the digastric muscle originates, based on *Didelphis marsupialis* (Turnbull, 1970). The anterior and lateral sides of the paracondylar process are in sutural contact with the petrosal. In fact, the medial end of the petrosal's ctp is raised and contributes to the base of the paracondylar process. Anterolateral to the paracondylar process are two foramina between the exoccipital and petrosal, the jugular foramen and, anteromedial to it, the foramen for the inferior petrosal sinus. Separating the two openings is a narrow, weak abutment of the exoccipital and petrosal. The surface of the exoccipital that contributes to the posteromedial border of both openings projects ventrally. The jugular foramen is oval and directed ventrally; the foramen for the inferior petrosal sinus is narrower and directed posterolaterally. Running posteriorly a short distance from the foramen for the inferior petrosal sinus is a weak sulcus. In the interval between these two foramina and the occipital condyle are two ovoid, anteriorly directed foramina for the hypoglossal nerve. The larger posterior

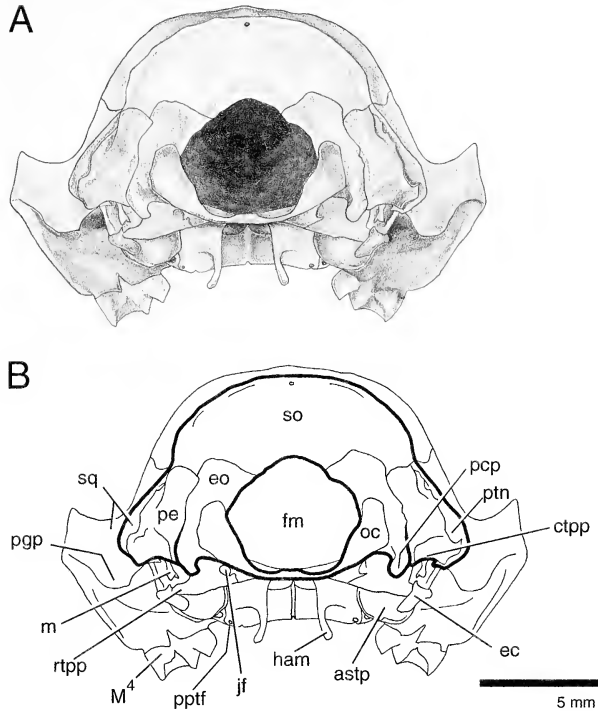


Fig. 9.—*Monodelphis brevicaudata* CM 52729, skull in occipital view excluding mandibles (A) with accompanying line drawing (B). Abbreviations: **astp**, alisphenoid tympanic process; **ctpp**, caudal tympanic process of the petrosal; **ec**, ectotympanic; **eo**, exoccipital; **fm**, foramen magnum; **ham**, pterygoid hamulus; **jf**, jugular foramen; **M⁴**, upper fourth molar; **m**, malleus; **oc**, occipital condyle; **pcp**, paracondylar process of the exoccipital; **pe**, petrosal; **pgp**, postglenoid process; **pptf**, foramen in the postpalatine torus; **ptn**, posttemporal foramen; **rtp**, rostral tympanic process of the petrosal; **so**, supraoccipital; **sq**, squamosal.

foramen is immediately in front of where the two articular surfaces of the occipital condyle meet, and the smaller anterior foramen lies anteromedial to that. Both hypoglossal foramina open into slight depressions.

In occipital view (Fig. 9), the vertical part of the exoccipital forms most of the lateral wall of the foramen magnum. It also bears the posterodorsal part of the saddle-shaped articular surface of the occipital condyle and the back of the paracondylar process. Laterally, the vertical part of the exoccipital contacts the mastoid exposure of the petrosal at a suture that is angled slightly dorsomedially. Dorsally, a remnant of the exoccipital's suture with the supraoccipital is preserved in CM 52729. It is a gently curved contact with the exoccipital convex and the supraoccipital concave. There are no foramina within the vertical part of the exoccipital.

Supraoccipital

The supraoccipital forms roughly the dorsal half of the occiput as well as the cap of the foramen magnum (Fig. 9). Its ventral border has narrow contacts with the paired mastoid exposures of the petrosal laterally and broader contacts with the paired exoccipitals medially. Its dorsal border is fused seamlessly with the interparietal (see above) and contributes to the posterior surface of the nuchal crest. The middle of the supraoccipital has

a gentle bulge over the vermis of the cerebellum. A similar bulge occurs in the dog, and dorsal to it and connected by a crest is a triangular projection, the external occipital protuberance (Evans, 1993). Neither protuberance nor crest occurs in *Monodelphis*. On the midline at the base of the nuchal crest is a small, round opening that contained dried blood in CM 52729 and was probably an emissary foramen. Given the uncertainty of the position of the interparietal-supraoccipital suture on the midline, it is unknown whether this foramen was entirely within the supraoccipital or between the supraoccipital and interparietal.

Mandible

The mandible houses the lower dentition: four incisors, a canine, three premolars, and four molars. It consists of a tooth-bearing horizontal part, or body, and a vertical part, or ramus (Fig. 2). The left and right mandibles are firmly united at the mandibular symphysis, a rough-surfaced fibrous joint. The mandibular symphysis extends from between the roots of the first incisors to the level of the p2–p3 embrasure (Fig. 3).

In lateral view (Fig. 2), the body of the mandible is thin, elongate, and tapered anteriorly; it achieves its maximum depth below m2. It is extremely thin below the incisors and, in fact, the roots of the incisors, canine, and first premolar are all slanted posteroventrally to a considerable degree. Because of the reduction in alveolar space, the root of the second incisor is wedged between that of its neighbors, producing the staggered condition (HersHKovitz, 1982, 1995) whereby the lateral side of the root is covered by a bony buttress that projects above the alveolar line of the adjacent teeth; this condition is not visible in the illustrations because of scale. The bulk of the mandibular body's dorsal surface is tooth bearing, but there is a narrow retromolar space between the last molar and the mandibular ramus (Figs. 2–3). The lateral (labial and buccal) surface of the body bears two subequal mental foramina (Fig. 2), both of which have weak, anterodorsally directed sulci emanating from them. The more anteriorly directed anterior mental foramen lies principally below the posterior root of p1; the more anterodorsally directed posterior mental foramen lies below the anterior root of m2. The medial (lingual) surface bears a subtle, smooth, longitudinal ridge below m3 and m4, which becomes slightly more prominent posterior to the molars on the mandibular ramus. This ridge ends posterodorsal to the mandibular foramen and corresponds in position to the mylohyoid line or crest of the dog (Evans, 1993). However, it apparently does not represent the attachment for the mylohyoid muscle, which is much closer to the ventral margin of the mandibular body and ramus in *Didelphis virginiana* (Hiemae and Jenkins, 1969). Based on *D. virginiana*, this line may represent the anteroventral limit of the attachment of the temporalis muscle. Ventral to and parallel with the "mylohyoid" line are two faint, narrow sulci that may be neurovascular impressions (mylohyoid nerve and vessels). The surface of the mandibular symphysis could not be studied in CM 52729, because the left and right mandibles remain connected. In a *M. brevicaudata* with separate mandibles, CM 76732, the surface of the symphysis is slightly roughened and cigar-shaped.

The ramus of the mandible bears three salient processes (Fig. 2): coronoid, condylar (articular), and angular. The coronoid process, the largest of the three, forms the dorsal part of the ramus and extends upward and outward. It is a large, thin plate of bone with a thickened, convex anterior border, the coronoid crest, and a concave posterior border. The dorsal surface of the coronoid process is rounded and comes to a posteriorly directed point at its posterodorsal limit. The ventral end of the posterior border of the coronoid process turns posteriorly into the condylar process, which buttresses the medial half of the transversely elongated, posterodorsally directed articular surface, the mandibular component of the temporomandibular joint (Fig. 3). The lateral half of the articular surface is buttressed by the posterior shelf of the masseteric fossa (Fig. 3; see below). The articular

surface lies above the occlusal plane, and in dorsal view, is roughly cigar-shaped. The angle of the mandible is the caudoventral part of the ramus. As is generally the case in marsupials, the angular process is medially inflected and, therefore, is best seen in dorsal (or ventral) view (Fig. 3). It is a triangular, posteromedially directed shelf that ends in a finger-like prong, which is concave dorsally and convex ventrally. Attaching to the ventral surface of the angular process is the superficial masseter muscle and to the dorsal surface is the internal pterygoid muscle, based on *Didelphis* (Hiiemae and Jenkins, 1969; Turnbull, 1970). In a recent study of the diversity of the marsupial angular process, Sánchez-Villagra and Smith (1997) classified the angular process of *Monodelphis brevicaudata* as rod-like, with the ratio of angular process shelf length to angular process length less than 0.72. The bulk of the lateral surface of the mandibular ramus in CM 52729 (Fig. 2) has a prominent, three-sided depression, the masseteric fossa for the insertion of the deep masseter and zygomaticomandibularis muscles, based on *D. marsupialis* (Turnbull, 1970). The anterior limit of the masseteric fossa is formed by the thickened coronoid crest, which also provides attachment for the temporalis muscle, based on *D. marsupialis* (Turnbull, 1970). The ventral limit of the masseteric fossa is formed by the masseteric line, the posterior part of which is expanded laterally to form the posterior shelf of the masseteric fossa (Marshall and Muizon, 1995), best seen in dorsal view (Fig. 3). On the medial side of the mandibular ramus, dorsal to the base of the angular process is the circular, posteriorly directed mandibular foramen (Fig. 3). The medial surface anterodorsal to the mandibular foramen provides a flat attachment area for the temporalis muscle, based on *D. marsupialis* (Turnbull, 1970). The external pterygoid muscle inserts on the medial side of the ventral-most excursion of the mandibular notch, which separates the coronoid and condylar processes, based on *Didelphis* (Hiiemae and Jenkins, 1969; Turnbull, 1970).

Dentition

Detailed descriptions of the dentition of *Monodelphis* are beyond the scope of this report. Reig et al. (1987:figs. 23 A, B, 24) provide detailed drawings of the upper and lower teeth of *M. domestica* FMNH 19504, in labial, occlusal, and lingual views and the upper and lower postcanine teeth of *M. orinoci* UKMNH 123941 in occlusal view. These authors do not describe the *Monodelphis* dentition per se, but numerous dental characters are found in their tables 1 and 2 and in the text.

DISCUSSIONS

As noted in the Introduction, few detailed descriptions of the skull of extant metatherians exist in the literature. Moreover, there are few detailed treatments of the major cranial foramina of extant metatherians, including the identification of contents and observation of variations. Perhaps the most thorough treatment of the major cranial foramina of extant metatherians is that by Archer (1976). This author (1976:figs. 2–4) illustrated the major extracranial arteries and veins in the dasyurids *Sminthopsis murina*, *Planigale maculata*, and *Antechinus stuartii*, based on dissections of latex injected specimens. He then described the basicranium and its major foramina in 17 genera of extant and extinct dasyuromorphians, including *Monodelphis dimidiata* based on WAM M6785 along with four other Recent genera of Didelphidae. Also included in Archer (1976:pp. 219–223) was a glossary of 21 major cranial foramina. Although generally a useful glossary, it is limited in the number of foramina included, the level of detail of contents considered, and the depth of variations described. In addition, some terminology employed by Archer (1976) is peculiar to Metatheria and is requiring of standardization for researchers studying other branches of the mammalian tree.

Following in Archer's (1976) footsteps, I include here a discussion of the major cranial foramina, their contents, and the variations encountered on the extracranial surfaces and on the isolated petrosals of the CM sample of *Monodelphis*. First, considered in alphabetical order are 37 named cranial foramina. For these foramina, I apply either an anglicized name from the fourth edition of the *Nomina Anatomica Veterinaria* (1994) or a name more widely used in the mammalian literature. The sources for the identification of contents of foramina are included. Ideally, identifications are based on studies of *Monodelphis domestica*, either published (e.g., Clark and Smith, 1993; Sánchez-Villagra and Wible, 2002) or my own unpublished observations. Second, considered in alphabetical order by cranial bone are the various small, unnamed foramina, some of which have been noted in the Descriptions. These foramina are of uncertain function, but the majority are likely nutrient or emissary foramina.

In addition to noting the distribution of these foramina in the CM sample of *Monodelphis*, I include observations on four other taxa: the didelphid *Didelphis albiventris* (CM 78203), the dasyurid *Dasyurus maculatus* (CM 50842), the early Paleocene metatherian *Pucadelphys andinus* (based on Marshall and Muizon, 1995), and the eutherian *Zalambdalestes lechei* from the Mongolian Late Cretaceous (based on Kielan-Jaworowska and Trofimov, 1981; Kielan-Jaworowska, 1984; Wible et al., in press). As a rough approximation, following the phylogenetic analysis of Rougier et al. (1998), foramina present in *Monodelphis* and *Didelphis* might be present in didelphids primitively; in these two taxa plus *Dasyurus* might be present in marsupials primitively; in these three taxa plus *Pucadelphys* might be present in metatherians primitively; and in these four taxa plus *Zalambdalestes* might be present in therians primitively. Regarding *P. andinus*, the absence of some of the unnamed foramina reported below should be taken with caution, because the basis is the descriptions by Muizon and Marshall (1995). These authors may not have investigated this extinct taxon to the same level of detail as done here or by Wible et al. (in press).

Named Cranial Foramina

Accessory Palatine Foramen.—In the dog (Evans, 1993), the accessory palatine nerve and artery, off the major palatine nerve and artery respectively, supply the caudal mucosa of the hard palate via foramina on the hard palate that are termed minor palatine foramina. Wible and Rougier (2000) argued that these foramina are best termed accessory palatine foramina, reserving the term minor palatine foramen for the aperture at the back of the palate that transmits the minor palatine nerve and artery to the soft palate. *Monodelphis breviceaudata* CM 52729 (Fig. 5) has a tiny foramen on the right side and two on the left asymmetrically arranged medial to the minor palatine foramen that may have been accessory palatine foramina. The number, size, and position of such apertures varies considerably in the CM sample. Only one specimen, *M. breviceaudata* (63509), has no foramina whatsoever on one side only. The remainder varies from a single tiny opening as on the right side in CM 52729 to a maximum of around 15 on one side in two *M. domestica* (80019, 80028).

Didelphis albiventris CM 78203 has two foramina on each side asymmetrically arranged resembling those in *Monodelphis*. *Dasyurus maculatus* CM 50842 has one small foramen on each side asymmetrically arranged and anteromedial to that more than 20 minute foramina of uncertain function. Foramina are not described for *Pucadelphys andinus* (Marshall and Muizon, 1995), and there are no accessory palatine foramina in *Zalambdalestes lechei* (Wible et al., in press).

Carotid Foramen (Entocarotid Foramen of Archer, 1976).—In *Monodelphis breviceaudata* CM52729 (Fig. 6), the carotid foramen lies entirely within the basisphenoid and, based

on *M. domestica* (Wible, unpubl. observ.), transmitted the internal carotid artery and accompanying vein and sympathetic nerve. This foramen exhibits no variability among the remaining CM specimens.

The carotid foramen is similarly situated in the basisphenoid in *Didelphis albiventris* CM 78203, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press). The carotid foramen is also within the basisphenoid in *Dasyurus maculatus* CM 50842, but it lies nearer the suture with the basioccipital and is recessed dorsally from the basicranial surface.

Condylod Canal.—Archer (1976) described a venous condylar foramen, which carries part of the venous drainage from the sigmoid sinus to the internal jugular vein in dasyurids. However, from Archer's labelled figures in Plate 1, it is apparent that his venous condylar foramen is the posterior hypoglossal foramen of this report. The dog has a condylod canal situated posterolateral to the hypoglossal foramen and transmitting the condylod vein, which connects the sigmoid sinus and the basilar sinus (Evans, 1993). In the ventral condylod fossa of *Monodelphis brevicaudata* CM 52729 (Fig. 6) are two hypoglossal foramina and no additional openings. However, the total absence of a condylod canal posterolateral to the two hypoglossal foramina is unusual in the CM specimens of *Monodelphis*, occurring in only one other *M. brevicaudata* (76730). In the remaining 37 specimens in which this feature could be examined on both sides, condylod canals medial to the paracondylar process are present bilaterally in 9 *M. brevicaudata* (4681, 52370, 65309, 68358, 68360, 68361, 76731, 76733, 76734), 15 *M. domestica* (80016, 80018, 80019, 80021, 80023, 80026–80030, 80035, 80036, 80039, 80040, 101529), one *M. dimidiata* (86608), and the two *M. osgoodi* (5242, 5248). Presence on one side only occurs in two *M. brevicaudata* (63510, 68359), seven *M. domestica* (5010, 80017, 80020, 80031, 80033, 80034, 80038), and one *M. dimidiata* (86609). The sample varies further in the relative size of the condylod canals and the occasional presence of two canals bilaterally or on one side only.

Condylod canals are not present in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press).

Ethmoidal Foramen.—According to Archer (1976), the ethmoidal foramen carries a branch of the internal carotid artery (presumably the ophthalmic artery) from the orbit into the nasal cavity in dasyurids. In *Monodelphis domestica* (Wible, unpubl. observ.), in addition to a branch of the ophthalmic artery it also carries the ethmoidal nerve, a branch of the ophthalmic division of the trigeminal nerve. The position of the ethmoidal foramen between the frontal and orbitosphenoid in *M. brevicaudata* CM 52729 (Fig. 4) is repeated in the remaining CM sample.

The ethmoidal foramen is similarly situated between the frontal and orbitosphenoid in *Didelphis albiventris* CM 78203 and *Dasyurus maculatus* CM 50842. It is said to be between the frontal, orbitosphenoid, and alisphenoid in *Pucadelphys andinus* (Marshall and Muizon, 1995) and within the frontal in *Zalambdalestes lechei* (Wible et al., in press).

Foramen for Frontal Diploic Vein (Frontal Foramen of Archer, 1976; Supraorbital Foramen of Marshall and Muizon, 1995).—According to Archer (1976), this foramen transmits the frontal diploic vein from the transverse frontal sinus to a branch of the external jugular vein in dasyurids. In the dog (Evans, 1993), the frontal diploic vein, an emissary vein from the diploë of the frontal bone to the ophthalmic vein, exits via a small unnamed foramen in the orbital surface of the postorbital process of the frontal (for the distribution in other eutherians, see Thewissen, 1989). In *Monodelphis brevicaudata* CM 52729 (Fig. 4), the foramen for the frontal diploic vein is small and lies within the frontal in the supraorbital

margin, anterior to the subtle postorbital process. In the remaining 53 CM *Monodelphis*, at least one bilaterally present foramen for the frontal diploic vein is invariably present. Variations include the size of the foramina and the number present. Double foramina occur bilaterally in one *M. brevicaudata* (76730) and one *M. domestica* (80016), and on one side only in two *M. brevicaudata* (68359, 76731) and four *M. domestica* (80021, 80032, 80036, 80037). The most unusual specimen was *M. domestica* (80040), which had three foramina (one large and two tiny) on the right and five tiny foramina on the left.

The foramen for the diploic vein is present in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Pucadelphys andinus* (Marshall and Muizon, 1995). *D. maculatus* differs in that it has two foramina on the right and three on the left. The diploic vein foramen is lacking in *Zalambdalestes lechei* (Wible et al., in press), but evidently occurs in the slightly older zalambdalestid *Kulbeckia kulbecke* (Archibald and Averianov, 2003).

Foramen for Greater Petrosal Nerve (Median Lacerate Foramen of Marshall and Muizon, 1995).—Based on sectioned specimens of *Monodelphis domestica* (Wible, unpubl. observ.), I identify the small aperture between the basisphenoid and petrosal that is confluent laterally with the much larger foramen ovale in *M. brevicaudata* CM 52729 (Fig. 6) as the foramen for the greater petrosal nerve. It transmits the greater petrosal nerve, a branch of the facial nerve, from the hiatus Fallopii to the posterior opening of the pterygoid canal. Variants in the CM *Monodelphis* sample concern the degree of separation from the foramen ovale, with the majority of specimens exhibiting the pattern of CM 52729. At one extreme are some *M. brevicaudata* (e.g., 8019, 80021) and *M. domestica* (e.g., 63510) in which the foramen for the greater petrosal nerve is nearly closed off from the foramen ovale by prongs extending posteriorly from the sphenoid and anteriorly from the petrosal, and at the other extreme are the two *M. osgoodi* (5242, 5248) with an extremely shallow foramen for the greater petrosal nerve that is barely recognizable as separate from the foramen ovale.

As noted by Marshall and Muizon (1995), Archer (1976) employed the term foramen pseudovalve in two different senses. Where the opening that I would identify as the foramen for the greater petrosal nerve is widely separated from the foramen ovale in the alisphenoid, as in the Tasmanian wolf *Thylacinus cynocephalus*, Archer (1976:pl. 1A) employed the term foramen pseudovalve for the former. Where the opening that I would identify as the foramen for the greater petrosal nerve is confluent with the foramen ovale between the alisphenoid and petrosal, as in the dasyurid *Dasyurus cristicauda*, Archer (1976:pl. 1C) employed the term foramen pseudovalve for the conjoined opening.

A foramen for the greater petrosal nerve is separate from the foramen ovale in *Didelphis albiventris* CM 78203 and *Pucadelphys andinus* (Marshall and Muizon, 1995), but is confluent with the latter opening in *Dasyurus maculatus* CM 50842. In *Zalambdalestes lechei* (Wible et al., in press), the greater petrosal nerve emerged from the cranial cavity via the posteriormost part of the piriform fenestra, the large gap between the petrosal, basisphenoid, and alisphenoid that is closed by membrane in extant forms (MacPhee, 1981).

Foramen for Inferior Petrosal Sinus (Internal Jugular Canal of Archer, 1976; Inferior Petrosal Foramen of Marshall and Muizon, 1995).—According to Archer (1976), this aperture leads the major internal jugular vein from the cranial cavity in dasyurids and does not carry a major artery, contra Gregory (1910) and Patterson (1965) who identified this opening as the posterior carotid canal. The occupant of this canal in didelphids (Dom et al., 1970; Wible, unpubl. observ.) as well as in dasyurids is not the internal jugular vein per se, but the inferior petrosal sinus (Sinus petrosus ventralis), which connects the cavernous sinus and the internal jugular vein. Consequently, I employ the more informative term

foramen for inferior petrosal sinus. In *Monodelphis brevicaudata* CM 52729 (Fig. 6) and the remaining CM sample, this foramen is situated between the exoccipital and petrosal, anterior to the jugular foramen.

A foramen for the inferior petrosal sinus separate from the jugular foramen occurs in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Pucadelphys andinus* (Marshall and Muizon, 1995), but not in *Zalambdalestes lechei* (Wible et al., in press).

Foramen Magnum.—According to Archer (1976), the foramen magnum carries the vertebral arteries, all or part of the sigmoid sinus to the vertebral sinus, cranial nerves, and the posterior part of the brain in dasyurids; presumably, the cranial nerves transmitted are the spinal roots of the accessory nerves, as in the dog (Evans, 1993). In *Monodelphis brevicaudata* CM 52729 (Fig. 9), the bulk of the foramen magnum is enclosed by the paired exoccipitals, with the basioccipital and supraoccipital contributing ventrally and dorsally, respectively. This pattern does not vary among the CM sample, with the following exceptions. Eleven *Monodelphis domestica* (80016, 80021, 80023, 80025–27, 80031, 80036, 80038, 101529, 101531) have a small, rod-shaped ossification that occupies the dorsal margin of the foramen magnum, either entirely separate from or in the process of fusing with the supraoccipital. This element was not reported by Clark and Smith (1993) in their study of cranial osteogenesis in *M. domestica*. It is unknown whether this element has fallen out of the remaining CM skulls or fails to form altogether. One *M. brevicaudata* (68358) has two small, rod-shaped elements in a comparable location, with the right one twice the size of the left.

The supraoccipital contributes to the dorsal border of the foramen magnum in *Didelphis albiventris* CM 78203, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press), whereas the exoccipitals exclude the supraoccipital from the dorsal border in *Dasyurus maculatus* CM 50842.

Foramen Ovale.—The didelphid foramen ovale transmits the mandibular division of the trigeminal nerve (Maier, 1987a; Wible, unpubl. observ.). In *Monodelphis brevicaudata* CM 52729 (Fig. 6), the foramen ovale is located between the alisphenoid and the lateral edge of the anteromedial flange of the promontorium of the petrosal; medially, the foramen ovale is continuous with a smaller opening, the foramen for the greater petrosal nerve, between the anterior edge of the anteromedial flange and the basisphenoid. As mentioned under the foramen for the greater petrosal nerve, variation in the CM sample concerns the degree of continuity between that aperture and the foramen ovale. For more discussion on the marsupial foramen ovale see Gaudin et al. (1996).

The foramen ovale is entirely within the alisphenoid in *Didelphis albiventris* CM 78203 and *Dasyurus maculatus* CM 50842, and between the alisphenoid, squamosal, and petrosal in *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Foramen Rotundum.—The foramen rotundum lies entirely within the alisphenoid and transmits the maxillary division of the trigeminal nerve in *Monodelphis domestica* (Clark and Smith, 1993). The only variant in the CM *Monodelphis* sample is on the right side of *M. dimidiata* (86609), in which there is a smaller, anterodorsally directed foramen situated immediately dorsal to the foramen rotundum. The specimen's left side preserves the dried zygomatic branch of the maxillary nerve, which leaves the dorsal margin of the foramen rotundum and is the likely occupant of the foramen on the right side. Archer (1976:p. 280) reported a small foramen of unknown function in *M. dimidiata* WAM M6785 piercing the alisphenoid "adjacent to dorso-lateral margin of foramen rotundum."

A foramen rotundum occurs in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei*

(Wible et al., in press). In the last three, as in *Monodelphis*, the foramen rotundum lies just posterolateral to the sphenorbital fissure, but in *D. albiventris* it lies more posteriorly, halfway between the sphenorbital fissure and foramen ovale.

Glaserian Fissure.—According to Klaauw (1931:p. 164), the fissura Glaseri develops first as an aperture in the anterior wall of the presumptive auditory bulla transmitting Meckel's cartilage, which disappears later in development; "Later on we find the chorda tympani nerve in it and often also the ramus inferior of the stapedial artery." As the components of the auditory bulla vary in mammals (Klaauw, 1931; Novacek, 1977), so do the components forming the glaserian fissure. In *Monodelphis brevicaudata* CM 52729, I have identified the glaserian fissure as a small notch or gap in the alisphenoid tympanic process, opposite the ventral end of the anterior process of the malleus (Fig. 6). Given that the ramus inferior is not present in marsupials (Wible, 1987), the chorda tympani is the sole occupant of this notch. Rather than a notch or gap, some CM specimens have a small foramen in the alisphenoid tympanic process, which is distributed as follows. In *M. brevicaudata*, a foramen is absent bilaterally (4681, 5061, 52730, 68360, 76731, 76733, 76734) or present on one side only (63509–11, 68358, 68359, 68361, 76730). In *M. domestica*, the foramen is absent bilaterally (5008, 5010, 80021, 80032, 80033, 80035), present on one side only (80017, 80024, 80025, 80032, 80033, 80035), or present bilaterally (80016, 80018, 80023, 80026–31, 80034, 80036–40). In *M. dimidiata*, the foramen is absent bilaterally (86609) or present bilaterally (86611). Finally, the foramen is absent in the one *M. osgoodi* (5242) that could be sampled.

In *Didelphis albiventris* CM 78203, the alisphenoid tympanic process has a deep notch for the chorda tympani nerve. The alisphenoid tympanic process is much larger in *Dasyurus maculatus* CM 50842 than in the didelphids. Near the process's contact with the anterior crus of the ectotympanic, there is a foramen for the chorda tympani on the right side and a notch on the left. An alisphenoid tympanic process is absent in both *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Hiatus Fallopii (Hiatus of Facial Canal of Archer, 1976).—In *Monodelphis* sp. CM 5024 (Fig. 7), the hiatus Fallopii is the gap in the petrosal at the anterior end of the cavum supracochleare. Based on *Didelphis virginiana* and *M. domestica*, the occupant of the cavum supracochleare is the geniculate ganglion of the facial nerve and the occupant of the hiatus Fallopii is the greater petrosal nerve (Wible, 1990; Sánchez-Villagra and Wible, 2002). Sánchez-Villagra and Wible (2002) identified three character states for the position of the hiatus Fallopii in isolated petrosals of metatherians: dorsal, intermediate, and ventral. In the dorsal state, the floor of the cavum supracochleare extends farther anteriorly than does the roof, whereas in the ventral state, the roof extends farther anteriorly than does the floor. In the intermediate state, the floor and roof extend anteriorly to the same extent. Sánchez-Villagra and Wible (2002) scored the intermediate state for *Monodelphis* sp. AMNH 133248. The two CM isolated petrosals exhibit different states: *Monodelphis* sp. CM 5024 has the intermediate state, whereas *M. brevicaudata* CM 5061 has the ventral state. However, the course of the greater petrosal nerve in both is the same, within the cranial cavity dorsal to the petrosal and exiting via the foramen for the greater petrosal nerve anterior to the petrosal.

The condition of the hiatus Fallopii could not be observed in *Didelphis albiventris* CM 78203 and *Dasyurus maculatus* CM 50842. Sánchez-Villagra and Wible (2002) scored the intermediate condition for *Didelphis* spp. and the ventral condition for *Dasyurus hallucatus*. In *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press), the hiatus Fallopii is at the anterior tip of the petrosal, the intermediate condition of Sánchez-Villagra and Wible (2002).

Hypoglossal Foramen (Condylod Foramen of Marshall and Muizon, 1995).—In the dog (Evans, 1993), there is a single hypoglossal foramen in the exoccipital that transmits the hypoglossal nerve and accompanying vein, which connects the condylod and vertebral veins. *Monodelphis brevicaudata* CM 52729 (Fig. 6) has anterior and posterior hypoglossal foramina in the exoccipital, with the latter the larger. Based on *Didelphis virginiana* and *M. domestica*, both these foramina transmit parts of the hypoglossal nerve and accompanying arteries and veins, with the arteries ultimately being branches of the vertebral artery (Wible, unpubl. observ.). In the remaining CM *Monodelphis* sample, all specimens in which the appropriate part of the exoccipital is visible have two hypoglossal foramina, but the relative sizes of the foramina vary. Most specimens of *M. brevicaudata* and *M. domestica* resemble CM 52729 in that the posterior is the larger foramen. However, in the two *M. osgoodi* (5242, 5248) and in some *M. brevicaudata* and *M. domestica*, the anterior is the larger.

Didelphis albiventris CM 78203 has two hypoglossal foramina, with the posterior one more than twice the size of the anterior one. The left side of *Dasyurus maculatus* CM 50842 also has two foramina, with the posteromedial one more than twice the size of the anterolateral; the specimen's right side has an additional small anteromedial foramen. *Pucadelphys andinus* (Marshall and Muizon, 1995) has three small, sub-equal hypoglossal foramina: posterior, anterolateral, and anteromedial. *Zalambdalestes lechei* (Wible et al., in press) has two hypoglossal foramina, with the anterior larger than the posterior.

Incisive Foramen (Anterior Palatine Vacuity of Osgood, 1921).—In *Monodelphis brevicaudata* CM 52729 (Fig. 5) and in the remainder of the CM sample, the elongate incisive foramen is on the anterior hard palate, largely within the premaxilla, but with the maxilla forming the posterior border. Sánchez-Villagra (2001) confirms that the nasopalatine duct communicates with the oral and nasal cavities as well as the vomeronasal organ in adult *M. domestica*, with the site of oral cavity communication being the incisive foramen. It is likely that the incisive foramen in *Monodelphis* also transmits blood vessels and nerves, as in the dog (i.e., the rostral septal branch of the major palatine artery and the septal branch of the caudal nasal nerve; Evans, 1993).

The incisive foramina in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Pucadelphys andinus* (Marshall and Muizon, 1995) resemble those in *Monodelphis* in size and position. They extend between the level of the upper third incisor and upper canine, and are largely within the premaxilla, with the maxilla forming the posterior border. The incisive foramina in *Zalambdalestes lechei* (Wible et al., in press) are very small, with the borders formed equally by the premaxilla and maxilla, and are unusual in that they are directed posteromedioventrally.

Infraorbital Foramen.—The anterior opening of the infraorbital canal on the face is the infraorbital foramen. The major occupant of the didelphid infraorbital canal is the infraorbital nerve, a branch of the maxillary division of the trigeminal nerve, with accompanying infraorbital artery and vein (Sánchez-Villagra and Asher, 2002). Variation in the CM *Monodelphis* sample concerns the position of the infraorbital foramen relative to the teeth; its posterior edge varies from dorsal to between the roots of P3 to dorsal to the posterior root of M1. It is between the roots of P3 in two *M. domestica* (80018, 80024) and one *M. sp.* (5002). It is dorsal to the posterior root of P3 in four *M. brevicaudata* (4681, 63509, 68358, 76731), 23 *M. domestica* (5008, 5010, 5025, 80016, 80017, 80021, 80023, 80025–32, 80034, 80036–40, 101529, 101531), the four *M. dimidiata* (86608–11), and one *M. sp.* (5024). It is dorsal to the P3–M1 embrasure (Fig. 2) in 9 *M. brevicaudata* (5061, 52729, 52730, 63510, 63511, 68359, 68361, 76730); over the anterior root of M1 in one *M. osgoodi* (5248), and over the posterior root of M1 in one *M. osgoodi* (5242). In those specimens retaining the upper deciduous third premolar (see

Appendix 2), the infraorbital foramen is dorsal to the anterior root of that tooth in two *M. domestica* (80033, 80035) and one *M. brevicaudata* (76732); between the roots of that tooth in two *M. domestica* (80019, 80020), and one *M. brevicaudata* (76733); and over the posterior root of that tooth in two *M. brevicaudata* (68360, 76734) and one *M. sp.* (5003).

The infraorbital foramen is dorsal to the anterior root of P3 in *Didelphis albiventris* CM 78203, the posterior root of M1 in *Dasyurus maculatus* CM 50842, P3 in *Pucadelphys andinus* (Marshall and Muizon, 1995), and the P2–P3 embrasure in *Zalambdalestes lechei* (Wible et al., in press).

Internal Acoustic Meatus.—The internal acoustic meatus in the isolated petrosals of *Monodelphis* CM 5024 (Fig. 7) and 5061 follows the pattern described for the dog by Evans (1993). In that form, the meatus is divided by a low transverse crest into dorsal and ventral parts. The dorsal part, the foramen acusticum superius, contains the opening of the facial canal for the facial nerve (the primary facial foramen of this report) and the cribriform dorsal vestibular area for the passage of some bundles of the vestibular nerve from the membranous labyrinth. The ventral part, the foramen acusticum inferius, contains the ventral vestibular area for additional bundles of the vestibular nerve that pass through a deep, tiny depression, the foramen singulare, and the spiral cribriform tract with perforations for the fascicles of the cochlear nerve.

Details of the internal acoustic meatus are not available for *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press).

Jugular Foramen (Posterior Lacerate Foramen of Archer, 1976).—According to Archer (1976), the jugular foramen in dasyurids transmits cranial nerves (presumably the glossopharyngeal, vagus, and accessory nerves as in didelphids [Wible, unpubl. observ.] and the dog [Evans, 1993]) and occasionally also a very small branch of the sigmoid sinus to the internal jugular vein. A venous channel does not pass through the jugular foramen in *Didelphis virginiana* (Wible, 1990; Wible and Hopson, 1995) and *Monodelphis domestica* (Wible, unpubl. observ.). Because this opening does not transmit the major contributor to the internal jugular vein, Archer (1976) opted for the usage of posterior lacerate foramen rather than jugular foramen. However, I employ the term jugular foramen, because it is more widely used in mammals, including the *Nomina Anatomica Veterinaria* (1994). Based on one juvenile *M. brevicaudata* (CM 68360) and several juvenile *M. domestica* (CM 80019, 80020, and 80033) in which sutures distinguish the basioccipital and exoccipitals, it is apparent that the jugular foramen lies between the exoccipital and the petrosal. No major variation in the jugular foramen was observed in the CM sample.

As in *Monodelphis*, the jugular foramen is small with a separate foramen for the inferior petrosal sinus anterior to it in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Pucadelphys andinus* (Marshall and Muizon, 1995). The jugular foramen is also small in *Zalambdalestes lechei* (Wible et al., in press), but there is no separate foramen for the inferior petrosal sinus.

Lacrimal Foramen.—According to Archer (1976), the lacrimal foramen carries the nasolacrimal duct and does not transmit any major blood vessel in dasyurids. In *Monodelphis brevicaudata* CM 52729 (Figs. 1, 2, 4) and in the remainder of the CM sample, with one exception, there are two lacrimal foramina on the facial process of the lacrimal bone. Each lacrimal foramen transmits a lacrimal canaliculus and accompanying vein; the canaliculi unite within the lacrimal bone to form the lacrimal sac out of which flows the nasolacrimal duct (M. Sánchez-Villagra, pers. commun.). The anteroventral foramen is slightly larger than the posterodorsal one. The sole variant is the left side of one *M. osgoodi* (5242) in which only a single large lacrimal foramen occurs. Sánchez-Villagra

and Asher (2002) reported more variation in the number of lacrimal foramina in other didelphids; they found that four out of five *Chironectes* and roughly two-thirds of 35 *Didelphis* have only one lacrimal foramen.

Didelphis albiventris CM 78203 and *Dasyurus maculatus* CM 50842 have two lacrimal foramina with the larger anteroventral one on the face and the posterodorsal one on the orbital rim. In contrast, *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press) have two lacrimal foramina within the orbit.

Major Palatine Foramen (*Maxillary Vacuity of Archer, 1976; Maxillopalatine Vacuity of HersHKovitz, 1992, 1997; Posterior Palatine Vacuity of Osgood, 1921*).—In the dog (Evans, 1993), the major palatine nerve and artery, branches off the maxillary artery and nerve, respectively, reach the palate via the major palatine foramen between the maxilla and palatine. In *Monodelphis brevicaudata* CM 52729 (Fig. 5) and the remainder of the CM sample, the major palatine foramen is elongated anteroposteriorly, extending the length of M1 and M2, and largely within the maxilla, with the palatine forming its narrow posterior border. Because of its size, the didelphid major palatine foramen is often referred to as a vacuity (Osgood, 1921; Archer, 1976; HersHKovitz, 1992, 1997).

In *Didelphis albiventris* CM 78203, the major palatine foramen is a large, irregular, assymetrical opening extending between the metacone of M3 and the protocone of M4, nearly completely within the palatine. On the left side of *Dasyurus maculatus* CM 50842, the major palatine foramen is a large opening, extending the length of M2, largely within the maxilla but with the palatine forming the posterior border; on the specimen's right side are two smaller foramina, a posterior one on the maxilla-palatine suture and a smaller anterior one within the maxilla. The major palatine foramen is unknown for *Pucadelphys andinus* (Marshall and Muizon, 1995). In *Zalambdalestes lechei* (Wible et al., in press), one or two major palatine foramina are in the maxilla opposite the penultimate premolar.

Mandibular Foramen.—In didelphids, the mandibular foramen transmits the inferior alveolar nerve off the mandibular division of the trigeminal nerve and accompanying blood vessels (Tandler, 1899; Wible, unpubl. observ.). In *Monodelphis brevicaudata* CM 52729 (Fig. 3) and the remainder of the CM sample, the mandibular foramen is located on the mandibular ramus, near the anterior root of the medially inflected angular process.

As in *Monodelphis*, the mandibular foramen is on the mandibular ramus near the anterior root of the medially inflected angular process in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Pucadelphys andinus* (Marshall and Muizon, 1995). In contrast, in *Zalambdalestes lechei* (Kielan-Jaworowska and Trofimov, 1981), the mandibular foramen is situated higher on the mandibular ramus and nearer the anterior border of the coronoid process. However, the mandibular foramen in the Early Cretaceous eutherian *Prokennalestes* resembles that in the metatherians in that it is just dorsal to the anterior root of the posteroventrally directed angular process (Kielan-Jaworowska and Dashzeveg, 1989).

Maxillary Foramen.—The posterior opening of the infraorbital canal within the orbit is the maxillary foramen. In *Monodelphis brevicaudata* CM 52729 and the remainder of the CM sample, with an exception, the maxillary foramen is bordered by the lacrimal dorsally and medially, and the maxilla laterally and ventrally, with a thin prong of palatine interposed between the lacrimal and maxilla. The variant is found in the two specimens of *M. osgoodi* (5242, 5248), in which the contribution of the palatine is considerably expanded, occupying the medial wall and sending a prong into the roof.

The bony borders of the maxillary foramen in *Dasyurus maculatus* CM 50842 and *Pucadelphys andinus* (Marshall and Muizon, 1995) resemble those described for *Monodelphis brevicaudata*. *Didelphis albiventris* CM 78203 differs from the other metatherians studied in that the palatine just barely contributes to the maxillary foramen and does not extend into the infraorbital canal. The maxillary foramen has no palatine

contribution in *Zalambdalestes lechei* (Wible et al., in press); it lies between the maxilla, lacrimal, and frontal.

Mental Foramen.—As in the dog (Evans, 1993), which usually has three mental foramina per side, the mental foramina in *Monodelphis* transmit branches of the inferior alveolar nerve and vessels (Wible, unpubl. observ.). *M. breviceaudata* CM 52729 (Fig. 2) has two mental foramina: the anterior under the posterior root of p1 and the posterior under the anterior root of m2. The CM sample exhibits considerable variability in the position of the mental foramina, some of which may be size related (see below).

Regarding the anterior foramen, the range of variation is between the anterior root of p1 and between the roots of p2. Only one *Monodelphis breviceaudata* (68361) has it below the anterior root of p1. In addition to CM 52729 (Fig. 2), only two other *M. breviceaudata* (63511 left only, 68358), nine *M. domestica* (80017, 80019–21, 80024, 80026, 80029, 80035, 101531), and one *M. sp.* (5003) have it below the posterior root of p1. Eight *M. domestica* (5025, 80018, 80031, 80033, 80034, 80036, 80039, 101529), two *M. dimidiata* (86608, 86610), and one *M. sp.* (5002) have it between p1 and p2. Twelve *M. breviceaudata* (4681, 5061, 52370, 63509, 63511 right only, 68359, 68360, 76730–34), twelve *M. domestica* (5008, 5010, 80016, 80023, 80025, 80027, 80028, 80030, 80032, 80037, 80038, 80040), two *M. dimidiata* (86609, 86611), one *M. osgoodi* (5248), and one *M. sp.* (5024) have it below the anterior root of p2. One *M. breviceaudata* (63510) and one *M. osgoodi* (5242) have it between the roots of p2. Finally, there are two specimens that have double anterior mental foramina on one side only: *M. domestica* (80018) and *M. dimidiata* (86610), between p1 and p2, and below the anterior root of p2.

Regarding the posterior foramen, the range of variation is between the anterior root of m1 to the anterior root of m2. In addition, there is considerably more left-right asymmetry with the posterior foramen. Only one side of one *Monodelphis breviceaudata* (63511) has it below the anterior root of m1. Four *M. breviceaudata* (63509, 63510 left only, 76732, 76733), seven *M. domestica* (5008 right only, 5010, 80016 left only, 80018, 80019, 80025 right only, 80035), the four *M. dimidiata* (86608–11), the two *M. osgoodi* (5242, 5248), and the three *M. sp.* (5002, 5003, 5024) have it between the roots of m1. Six *M. breviceaudata* (4681, 68359 left only, 68360, 68361, 76731, 76734) and 19 *M. domestica* (5008 left only, 5025, 80016 right only, 80020, 80021, 80023, 80024, 80025 left only, 80026, 80027 left only, 80028, 80030, 80033, 80034, 80038, 80039 left only, 80040, 101529, 101531) have it below the posterior root of m1. Three *M. breviceaudata* (5061, 63510 right only, 63511 right only) and four *M. domestica* (80032, 80036 left only, 80037, 80039 right only) have it below the m1–m2 embrasure. In addition to CM 52729 (Fig. 6), only three other *M. breviceaudata* (52370, 68358, 76730) and five *M. domestica* (80017, 80027 right only, 80029, 80031, 80036 right only) have it below the anterior root of m2. One *M. breviceaudata* (68359) has two posterior mental foramen on the right side only at the anterior root of m1 and at the m1–m2 embrasure.

In addition to the anterior and posterior mental foramina, two specimens have a middle mental foramen: *Monodelphis breviceaudata* (4681) at the posterior root of p3 and *M. domestica* (80037) at the anterior root of p3.

There appears to be a stronger correlation between posterior mental foramen position and size. The posterior mental foramen is anteriorly positioned (e.g., between the roots of m1) in six of the nine specimens retaining the lower deciduous third premolar, *Monodelphis breviceaudata* (68360, 76733, 76734), *M. domestica* (80019, 80035), and *M. sp.* (5003), as well as the adult *M. dimidiata* (86608–11) and *M. osgoodi* (5242, 5248), which have the smallest adult skulls (with m4 erupted) in the CM sample (see Appendix 2). The anterior mental foramen in these same specimens ranges from below the posterior root of p1 (5003,

80019, 80035), to between p1 and p2 (80018, 86608, 86610), to below the anterior root of p2 (5248, 68360, 76733, 76734, 86609, 86611), to between the roots of p2 (5242).

Didelphis albiventris CM 78203 has only one mental foramen, below the p1–p2 embrasure. *Dasyurus maculatus* CM 50842, which unlike the didelphids and *Pucadelphys andinus* has only two premolars, has three mental foramina, asymmetrically arranged. On the left they are below the anterior root of the first premolar, the posterior root of the m1, and the m1–m2 embrasure; on the right they are below the posterior root of the first premolar, the posterior root of the second premolar, and the posterior root of the m1. *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Kielan-Jaworowska and Trofimov, 1981) have two mental foramina: below the p1 and m1 in the former, and below the anterior root of the first premolar and between the roots of the third (penultimate) premolar in the latter.

Minor Palatine Foramen (*Postero-Lateral Palatine Foramen* of Archer, 1976; *Posterolateral Vacuity or Foramen* of Hershkovitz, 1992, 1997; *Postpalatine Foramen* of Marshall and Muizon, 1995).—In the dog (Evans, 1993), the minor palatine nerve and artery, branches of the maxillary nerve and artery, respectively, leave the orbit and reach the palate via an unnamed notch that rarely closes to a foramen in the posterior margin of the maxilla and palatine. In *Monodelphis brevicaudata* CM 52729 (Fig. 5) and in the remainder of the CM sample, the minor palatine foramen is obliquely oriented, posteromedial to the last upper molar, and within the maxillopalatine suture.

The minor palatine foramen in *Didelphis albiventris* CM 78203, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press) resembles that in *Monodelphis*. The foramen in *Dasyurus maculatus* CM 50842 is similarly situated, but the posterior border is partially open, as bony prongs projecting from the maxilla and palatine do not meet.

Parietal Foramen.—A small emissary foramen in the parietal, near the midline, is variably present in humans and some other anthropoid primates (Boyd, 1930, 1934). *Monodelphis brevicaudata* CM 52729 (Fig. 1) has one small emissary foramen near the midline in the right parietal. The presence and number of similar parietal foramina in the remaining CM sample is variable. No foramina occur in four *M. brevicaudata* (5061, 63509, 63511, 76732), eight *M. domestica* (5008, 5025, 80024, 80031, 80033, 80035, 80038, 80039), and the four *M. dimidiata* (86608–11). The remaining specimens have between a single foramen on one side only to the maximum in *M. brevicaudata* CM 76730 of six on the right side and nine on the left.

Didelphis albiventris CM 78203 has three tiny parietal foramina off the midline on each side, whereas *Dasyurus maculatus* CM 50842 has two on each side. Parietal foramina are not described or illustrated for *Pucadelphys andinus* (Marshall and Muizon, 1995) and are absent in *Zalambdalestes lechei* (Wible et al., in press).

Postglenoid Foramen.—According to Archer (1976), the postglenoid foramen in dasyurids carries the postglenoid vein as well as the vein of the suprameatal foramen and the postglenoid artery, a branch of the external carotid that reaches the temporal fossa via the suprameatal foramen. This same pattern occurs in *Didelphis virginiana* (Wible, 1987, 1990) and *Monodelphis domestica* (unpubl. observ.), except that the vein exiting the postglenoid foramen is identified as the sphenoparietal emissary vein, following Gelderen (1924). This is in contrast to the capsuloparietal emissary vein exiting the postglenoid foramen in placentals, which has a different developmental history (Gelderen, 1924; Wible, 1990). In *M. brevicaudata* CM 52729 (Fig. 6), the postglenoid foramen is entirely within the squamosal, although the anterior crus of the ectotympanic approaches the medial margin. Also, three openings are visible within the substance of the postglenoid foramen, with the posterior and largest of these three being the channel for the sphenoparietal

emissary vein; the anterior two are postzygomatic foramina. Checking the number of openings within the substance of the postglenoid foramen in the remaining CM sample was difficult, because soft tissue frequently obstructs this area. In *M. brevicaudata*, some specimens have four openings (63510, 68359, 68631) and others five (63509, 63511, 76734).

The postglenoid foramen of *Dasyurus maculatus* CM 50842 is positioned as that in *Monodelphis*. In *Didelphis albiventris* CM 78203, the foramen is more anteriorly situated, medial to the postglenoid process rather than posterior. The postglenoid foramen also differs positionally in both *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press). The aperture in the former is more laterally placed, on the posterior root of the zygomatic arch, and in the latter is more anteriorly placed, within the glenoid fossa, anterior to the postglenoid process.

Posttemporal Notch.—The mammalian posttemporal foramen lies on the occiput usually between the petrosal and squamosal, and transmits the arteria diploëtica magna and accompanying vein (Wible, 1987; Wible and Hopson, 1993, 1995). This aperture and its arterial and venous contents have been identified in the ventrolateral margin of the occiput of *Didelphis virginiana* (Wible, 1990; Wible and Hopson, 1995). In *Monodelphis brevicaudata* CM 52729 (Fig. 9), rather than a distinct posttemporal foramen, there is a notch in the ventrolateral mastoid exposure of the petrosal in the suture with the squamosal (see also Fig. 7). This notch certainly did not transmit any substantial structure, and it is unclear whether it transmitted any vessel at all. In the remaining CM sample, a posttemporal notch is present bilaterally in the mastoid exposure of the vast majority of specimens. However, the notch is present on one side only in two *M. brevicaudata* (5061, 63511) and three *M. domestica* (80032, 80033, 80034), and is absent bilaterally in three *M. domestica* (80016, 80019, 80035) and the two *M. osgoodi* (5242, 5248). In one *M. brevicaudata* (63509), there is a distinct posttemporal foramen entirely within the mastoid exposure on the right side; the left side has only a posttemporal notch.

In *Didelphis albiventris* CM 78203, the posttemporal notch is present, does not appear to be patent, and is situated more dorsally (nearer the supraoccipital bone) than in *Monodelphis*. On the right side of *Dasyurus maculatus* CM 50842, a minute foramen is situated in the middle of the suture between the mastoid exposure and squamosal; on the specimen's left side, this tiny opening is entirely within the petrosal. *Pucadelphys andinus* (Marshall and Muizon, 1995) has a posttemporal foramen in the position of the posttemporal notch of *Monodelphis*. *Zalambdalestes lechei* (Wible et al., in press) has a posttemporal foramen in the position of the notch of *D. albiventris*.

Postzygomatic Foramen (Gregory, 1910).—According to Archer (1976), the postzygomatic foramen in dasyurids carries a vein out of the squamosal root of the zygomatic arch to the postglenoid vein. *Monodelphis brevicaudata* CM 52729 (Fig. 6) has two postzygomatic foramina visible in the anterior wall of the postglenoid foramen. As noted with the postglenoid foramen, checking the number of openings within the substance of that aperture in the CM sample was difficult, because soft tissue frequently obstructs this area. In *M. brevicaudata*, some specimens have three postzygomatic foramina (63510, 68359, 68631) and others four (63509, 63511, 76734).

The left side of *Didelphis albiventris* CM 78203 has three postzygomatic foramina visible within the postglenoid foramen; the specimen's right side has four. The left side of *Dasyurus maculatus* has one tiny postzygomatic foramen within the postglenoid foramen; the specimen's right side has two tiny openings. Postzygomatic foramina are not described in *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Marshall and Muizon (1995:figs. 12A, 17) identified the opening on the posterolateral aspect of the postglenoid process in *Pucadelphys andinus* as the postzygomatic foramen; *Monodelphis brevicaudata* CM 52729 (Fig. 4) has a similar aperture discussed with the squamosal bone below that I have not named. Although Archer (1976) did not fully describe the position of the postzygomatic foramen, Gregory (1910) described it as opening "below or within the lip of the postglenoid foramen." It is the sense of Gregory that I employ the term here.

Primary Facial Foramen.—Following Wible (1990) and Wible and Hopson (1993), the primary facial foramen is the opening on the endocranial surface of the petrosal that transmits the facial nerve from the internal acoustic meatus to the cavum supracochleare. In *Monodelphis* sp. CM 5024 (Fig. 7) and *M. brevicaudata* CM 5061, the primary facial foramen lies within the foramen acusticum superioris, anterior to the dorsal vestibular area.

The primary facial foramen could not be studied in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Zalambdalestes lechei* (Wible et al., in press). The foramen in *Pucadelphys andinus* (Marshall and Muizon, 1995) resembles that in *Monodelphis*.

Prootic Canal (Canal for the Lateral Head Vein of Wible and Hopson, 1995).—According to Wible (1990) and Rougier and Wible (in press), the metatherian prootic canal is a narrow, horizontal canal in the petrosal that connects the groove for the prootic sinus on the lateral surface with the facial sulcus on the ventral surface. As pointed out recently by Rougier and Wible (in press), it is uncertain whether the vein that occupies this canal in metatherians is the prootic sinus or the lateral head vein, because the vein that serves to distinguish these two, the post-trigeminal vein, involutes in early ontogenetic stages. Sánchez-Villagra and Wible (2002) divided the metatherian prootic canal into two characters: the presence/absence of the tympanic aperture and the presence/absence of the lateral aperture. Among extant metatherians, both apertures are found in most didelphids (*Glironia venusta* and *Thylamys* spp. have only the lateral aperture), and some caenolestids, dasyuromorphians, phalangerids, and pseudocheirids. These authors' observation of both apertures for *Monodelphis* sp. was based on AMNH 133248. *Monodelphis* sp. CM 5024 has both apertures (Fig. 7). In *M. brevicaudata* CM 5061, the ventral aperture cannot be confirmed, because the appropriate area is covered by soft tissue; the lateral aperture is present and is more than double the diameter of the same opening in CM 5024.

The prootic canal in *Didelphis albiventris* CM 78203 and *Pucadelphys andinus* (Marshall and Muizon, 1995) resembles that in *Monodelphis*. The presence/absence of the prootic canal could not be ascertained in *Dasyurus maculatus* CM 50842 because the auditory bulla conceals the middle ear; Sánchez-Villagra and Wible (2002) reported it to be absent in *D. hallucatus*. As in most eutherians, the prootic canal is absent in *Zalambdalestes lechei* (Wible et al., in press); an exception within Eutheria is *Prokennalestes* from the Mongolian Early Cretaceous, which has a short, vertical prootic canal (Wible et al., 2001).

Pterygoid Canal.—In the dog (Evans, 1993), the pterygoid canal lies in the suture between the pterygoid and basisphenoid and transmits the nerve and artery of the pterygoid canal from the skull base to the posteroinferior floor of the orbit. The nerve of the pterygoid canal enters the canal's basicranial aperture and is composed of sympathetic fibers from the internal carotid (deep petrosal) nerve and parasympathetic fibers from the greater petrosal nerve; the artery enters the orbital aperture and is a branch of the maxillary artery. According to Wible (1984), the metatherian pterygoid canal transmits nerves, but no artery. In *Monodelphis brevicaudata* CM 52729 (Fig. 6) and in the remainder of the CM sample, the basicranial aperture of the pterygoid canal is between the basisphenoid and pterygoid,

anterior to the carotid foramen and medial to the entopterygoid crest; the orbital aperture is between the alisphenoid and pterygoid, in the floor of the sphenorbital fissure.

The pterygoid canal in *Didelphis albiventris* CM 78203 is relatively shorter than that in *Monodelphis*, and the anterior and posterior apertures are slightly different. The anterior aperture is in the floor of the sphenorbital fissure, but between the palatine and alisphenoid; the posterior aperture is between the basisphenoid and pterygoid, but is more anteriorly positioned, just posterior to the level of the foramen rotundum. The apertures of the pterygoid canal in *Dasyurus maculatus* CM 50842 differ from those of the didelphids. The anterior aperture is more anteriorly positioned, just in front of the sphenorbital fissure in the suture between the palatine and alisphenoid; the posterior aperture is more laterally positioned, beneath the entopterygoid process, just posterior to the foramen rotundum. The condition of the pterygoid canal in *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press) is unknown.

Secondary Facial Foramen.—Following Wible (1990) and Wible and Hopson (1993), the secondary facial foramen is the opening on the tympanic surface of the petrosal that transmits the facial nerve from the cavum supracochleare into the middle ear. In *Monodelphis* sp. CM 5024 (Fig. 7) and *M. breviceaudata* CM 5061, the secondary facial foramen lies anterior to the fenestra vestibuli and the tympanic aperture of the prootic canal.

The disposition of the secondary facial foramen in *Didelphis albiventris* CM 78203 and *Pucadelphys andinus* (Marshall and Muizon, 1995) is as in *Monodelphis*. The condition in *Dasyurus maculatus* CM 50842 could not be studied because the auditory bulla conceals the middle ear. The secondary facial foramen of *Zalambdalestes lechei* (Wible et al., in press) differs from that of the metatherians in that it is more posteriorly positioned, just in front of the fenestra vestibuli.

Sphenopalatine Foramen.—In the dog (Evans, 1993), there are two openings in the orbital process of the palatine, the sphenopalatine foramen, which transmits the caudal nasal nerve and sphenopalatine artery and vein off the maxillary nerve, artery, and vein, respectively, and the caudal palatine foramen, which transmits the major palatine nerve and artery to the palatine canal. In *Monodelphis breviceaudata* CM 52729 (Fig. 4) and the remainder of the CM sample, only a single opening is present in the orbital process of the palatine serving the function of the two in the dog. I identify the one foramen in *Monodelphis* as the sphenopalatine foramen, following, for example, Archer (1976), the Nomina Anatomica Veterinaria (1994), and Marshall and Muizon (1995).

The sphenopalatine foramen of *Didelphis albiventris* CM 78203 and *Pucadelphys andinus* (Marshall and Muizon, 1995) resembles that of *Monodelphis*; it lies anterodorsal to the minor palatine foramen, within the palatine. In *Dasyurus maculatus* CM 50842, the sphenopalatine foramen is also within the palatine, but more anteriorly placed, near the maxillary foramen. In *Zalambdalestes lechei* (Wible et al., in press), the sphenopalatine foramen is anterodorsal to the minor palatine foramen, but between the palatine, frontal, and maxilla.

Sphenorbital Fissure (Optic-Orbital Foramen of Marshall and Muizon, 1995).—In therians, the term sphenorbital fissure has been employed for the large gap in the medial wall of the orbit between the orbitosphenoid and alisphenoid that transmits nerves and vessels from the cavum epiptericum (Gregory, 1910; McDowell, 1958; Archer, 1976). The nervous and vascular contents of this opening vary dramatically among extant therians and may include some combination of the following: the optic, oculomotor, trochlear, ophthalmic, maxillary, and abducens nerves; the ramus infraorbitalis, arteria anastomotica, and ophthalmic artery; and the ophthalmic veins. In marsupials, the usual contents are the optic, oculomotor, trochlear, ophthalmic, and abducens nerves, and the ophthalmic artery and veins (Kuhn and Zeller, 1987; Wible and Rougier, 2000). In *Monodelphis breviceaudata* CM 52729 (Fig. 4) and the remainder of the CM sample, the sphenorbital fissure is situated

between the orbitosphenoid, alisphenoid, pterygoid, palatine, and presphenoid. In contrast to metatherians, eutherians have a separate optic foramen and their sphenorbital fissure is often referred to as the superior orbital fissure to distinguish it from the metatherian condition (Wible et al., in press).

The sphenorbital fissure of *Didelphis albiventris* CM 78203 and *Dasyurus maculatus* CM 50842 differs from that of *Monodelphis* in that there is no contribution from the pterygoid bone. In *Pucadelphys andinus* (Marshall and Muizon, 1995), the sphenorbital fissure lies between the palatine, orbitosphenoid, frontal, and alisphenoid. The corresponding aperture in *Zalambdalestes lechei* (Wible et al., in press) is between the alisphenoid and orbitosphenoid.

Subsquamosal Foramen.—Wible et al. (in press) employed the term subsquamosal foramen for vascular apertures in the squamosal dorsal to the suprameatal bridge. Unfortunately, Archer (1976) used the same term for the suprameatal foramen of this report. Despite the potential confusion, I continue to employ the term subsquamosal foramen in the sense of Wible et al. (in press). *Monodelphis brevicaudata* CM 52729 (Fig. 2) has no subsquamosal foramina, but it is unusual in that absence among the remaining CM sample. In addition to CM 52729, subsquamosal foramina are lacking in two other *M. brevicaudata* (63509, 63510), three of the four *M. dimidiata* (86608–10), and the two *M. osgoodi* (5242, 5248). The remaining twelve *M. brevicaudata* and one *M. dimidiata* (86611), and the 28 *M. domestica* preserving the squamosal have between one and a dozen small subsquamosal foramina.

Didelphis albiventris CM 78203 has six tiny subsquamosal foramina and *Dasyurus maculatus* CM 50842 has but one tiny opening. Subsquamosal foramina are not described or illustrated for *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press) has one large subsquamosal foramen, immediately dorsal to the suprameatal bridge.

Suprimeatal Foramen (Subsquamosal Foramen of Archer, 1976).—Based on didelphids (Wible, 1987) and dasyurids (Archer, 1976), the suprimeatal foramen in the metatherian squamosal, dorsal to the external acoustic meatus, carries a temporal branch of the postglenoid artery and accompanying vein to the temporal fossa. Wible (1987) identified this as a ramus temporalis of the stapedial artery system. *Monodelphis brevicaudata* CM 52729 (Fig. 4) has a posterolaterally directed suprimeatal foramen, which is continuous through the squamosal with the postglenoid foramen (Fig. 6). Posterior to the suprimeatal foramen is a depression, which dorsally includes a short, posterodorsally directed sulcus for the ramus temporalis (Fig. 2). The main variant in the CM sample concerns the relative size of the suprimeatal foramen. In three *M. brevicaudata* (68358, 68361, 76732) and one *M. sp.* (5024), the suprimeatal foramen is comparable in size to that of CM 52729. In all the remaining specimens that could be sampled, the 29 *M. domestica*, the four *M. dimidiata*, the two *M. osgoodi*, and the 11 remaining *M. brevicaudata*, 5061, the suprimeatal foramen is roughly twice as big, expanding posteriorly into the area where the depression is present in CM 52729.

Didelphis albiventris CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press) have a suprimeatal foramen resembling that in *Monodelphis brevicaudata* CM 52729.

Stylomastoid Notch.—In the dog (Evans, 1993), the stylomastoid foramen is the opening between the petrosal, the osseous bulla, and the tympanohyal cartilage by which the facial nerve leaves the middle ear and by which the stylomastoid artery off the posterior auricular artery enters. Archer (1976) reported for dasyurids that the stylomastoid foramen does not appear to transmit any major vessel; this is the case in *Didelphis virginiana* and *Monodelphis domestica* (Wible, unpubl. observ.). In *M. sp.* CM 5024 (Fig. 7A, D) and the

remainder of the CM sample, there is no stylomastoid foramen, but a notch bordered by the tympanohyal anteriorly and the caudal tympanic process of the petrosal posteriorly.

Didelphis albiventris CM 78203, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press) have a stylomastoid notch resembling that in *Monodelphis* sp. CM 5024. In contrast, *Dasyurus maculatus* CM 50842 has a stylomastoid foramen between the squamosal and petrosal.

Transverse Canal Foramen.—The metatherian transverse canal has been reviewed recently by Sánchez-Villagra and Wible (2002). They reported that most extant metatherians have a transverse canal foramen in the basisphenoid that transmits a vein communicating with the cavernous sinus and that in some forms this vein communicates across the midline with its antimeres (see also Archer, 1976). Sánchez-Villagra and Wible (2002) recorded two characters for the transverse canal: the presence/absence and position of the transverse canal foramen, and the presence/absence of an intramural canal between the right and left transverse canal foramina. *Monodelphis* sp. was scored as having the transverse canal foramen anterior to the carotid foramen (as compared with confluent with the carotid foramen or perforating the pterygoid fossa) and with an intramural canal. Their observation of the position of the transverse canal foramen is congruent with that in *M. brevicaudata* CM 52729 (Fig. 6) and the remainder of the CM sample. I did not confirm the presence of an intramural canal.

Didelphis albiventris CM 78203 has a transverse canal foramen resembling that in *Monodelphis*. The foramen in *Dasyurus maculatus* CM 50842 differs from the didelphids in that it is laterally directed rather than posterolaterally directed. The transverse canal foramen is absent in *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Unnamed Cranial Foramina

Alisphenoid.—*Monodelphis brevicaudata* CM 52729 (Fig. 6) has a small opening in the ventromedial margin of the tympanic process of the left alisphenoid; on the right side, only a notch exists. Only two other *M. brevicaudata* have comparable openings in the ventromedial aspect of the alisphenoid tympanic process: CM 76732 has a small opening on the right side only and CM 4681 has three small openings on the left side only. It is possible that these are not true foramina, but merely unossified areas in the auditory bulla.

Nearer the glaserian fissure, *Didelphis albiventris* CM 78203 has a deep, narrow notch in the alisphenoid tympanic process. Anterior to this notch on the left side are two tiny foramina and on the right side are three. The function of these structures is unknown. *Dasyurus maculatus* CM 50842 has nothing comparable, and the alisphenoid tympanic process is absent in *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Lacrimal.—*Monodelphis brevicaudata* CM 52729 has a small, anteriorly directed foramen in the orbital process of the lacrimal dorsal to the maxillary foramen on the right side and two such openings on the left. A single opening is present bilaterally in the majority of the remaining CM sample, i.e., in 38 of 51 that could be sampled. However, no foramina occur in one *M. domestica* (80028) and one *M. dimidiata* (86610), and are absent on one side only in one *M. brevicaudata* (68360), one *M. dimidiata* (86608), and four *M. domestica* (80024, 80025, 20027, 80031). A third *M. dimidiata* (86609) preserves only the left lacrimal and it has no foramen. As in CM 52729, two foramina on one side and a single on the other are found in three other *M. brevicaudata* (63511, 76733, 76734) and one *M. domestica* (80023). Two foramina are present bilaterally in one *M. sp.* (5003). The two *M. osgoodi* (5242, 5248) present additional variants. Neither specimen has a foramen in the

lacrimal directly over the maxillary foramen; however, CM 5242 has a small foramen within the orbit at the level of the lower lacrimal foramen on the right side only, and CM 5248 has a tiny foramen at the level of the upper lacrimal foramen on the right side only and posterodorsal to that a second tiny foramen that is bilaterally present.

The right side of *Didelphis albiventris* CM 78203 has a foramen in the lacrimal immediately dorsal to the maxillary foramen; it is subequal in size to the upper lacrimal foramen. There is no foramen on the specimen's left side. The left side of *Dasyurus maculatus* CM 50842 has a tiny opening halfway between the maxillary foramen and upper lacrimal foramen; the right side has no foramen. Similar foramina are not reported for *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Maxilla.—*Monodelphis breviceaudata* CM 52729 (Fig. 2) has several small foramina on the facial process of the maxilla anterior to the infraorbital foramen. The foramen anterodorsal to the infraorbital foramen, dorsal to P2 is present bilaterally in the remaining 15 specimens of *M. breviceaudata*. Variants include a single foramen on one side and double on the other (4681, 5061), double on both sides (76732–34), and double on one side, triple on the other (63509, 76730). In *M. domestica*, this foramen is absent bilaterally (80028, 80035), absent on one side only (5008, 5010, 5025, 80016, 80018, 80024, 80033, 80038, 101529), present bilaterally (80019–21, 80023, 80026, 80027, 80029–32, 80034, 80036, 80039, 80040), double on one side, single on the other (80017, 80025, 80037), or double bilaterally (101531). A further variant in *M. domestica* is the appearance of a foramen at the level of the infraorbital foramen, dorsal to P3; this is present one side only (80018, 80026, 80033) or present bilaterally (80032). In *M. dimidiata*, the foramen anterodorsal to the infraorbital foramen is present bilaterally (86608, 86611), on one side only (86609), or absent bilaterally (86610). The foramen is absent in the two *M. osgoodi* (5242, 5248) and one *M. sp.* (5024), and present on one side only in the remaining two *M. sp.* (5002, 5003). The left side of *M. osgoodi* (5248) has a foramen dorsal to P3 rather than P2.

Didelphis albiventris CM 78203 has a foramen dorsal to the diastema between the P1 and P2 near the nasal bone; it is subequal in size to the upper lacrimal foramen. The left side of *Dasyurus maculatus* CM 50842 has a tiny opening dorsal to the ultimate premolar–M1 embrasure near the nasal bone; a comparable opening is not present on the right side. Similar foramina in the maxilla are not reported for *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Orbitosphenoid.—No foramina are found in the orbitosphenoid in *Monodelphis breviceaudata* CM 52729 (Fig. 4). However, a small foramen occurs in the posteroventral base of the orbitosphenoid, just anterior to the sphenorbital fissure in 31 of the remaining 41 CM specimens that could be sampled. This foramen is present bilaterally in *M. domestica* (80018, 80037, 101529), *M. dimidiata* (86608), and *M. sp.* (5002), and on one side only in *M. breviceaudata* (68359, 68360, 76730–34), *M. domestica* (5008, 80016–19, 80021, 80023, 80025, 80027, 80029–33, 80035, 80036, 80040), *M. dimidiata* (86611), and *M. sp.* (5003). Of the specimens listed, this foramen is double on one side only in one *M. breviceaudata* (68360) and seven *M. domestica* (80016, 80018, 80023, 80025, 80027, 80037, 101529). A foramen in the orbitosphenoid is absent bilaterally in five *M. breviceaudata* (4681, 52730, 63509–11, 68358), four *M. domestica* (5010, 80020, 80026, 80038), and one *M. sp.* (50024).

Similar foramina are not present in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press).

Palatine.—In addition to the named foramina in the palatine detailed above, *Monodelphis breviceaudata* CM 52729 has unnamed foramina through the postpalatine

torus and in the orbital process. The small foramen through the postpalatine torus is posteromedial to the minor palatine foramen, connects the hard palate and choanae, and is visible in occipital view (Fig. 9). There are three foramina within the orbital process (Fig. 4): one immediately posterior to the sphenopalatine foramen and two more posteriorly connecting the orbital fossa with the choanae: one at the level of the anterior edge of the ethmoidal foramen and the other anterodorsal to that near the suture with the frontal. Finally, there is an elongate, irregular gap situated posterior to the palatine, between that bone and the pterygoid (Fig. 4).

A foramen through the postpalatine torus is ubiquitous in the remaining 52 CM specimens that could be sampled. Variation in this feature concerns the degree of ventral closure. Both closed foramina and deep notches are present within individuals of *Monodelphis breviceaudata*, *M. domestica*, and *M. dimidiata*. The two *M. osgoodi* (5242, 5248) exhibit the same unusual state: they are the only specimens that have shallow notches. A similar foramen through the postpalatine torus occurs in *Didelphis albiventris* CM 78203 and *Zalambdalestes lechei* (Wible et al., in press); rather than a foramen, *Dasyurus maculatus* CM 50842 has a notch, and neither a foramen nor a notch is reported for *Pucadelphys andinus* (Marshall and Muizon, 1995).

One or more tiny foramina posterior to the sphenopalatine foramen are present bilaterally in 38 of the 41 remaining CM specimens that could be sampled. The three exceptions are two *Monodelphis dimidiata* (86608, 86609) and one *M. sp.* (5003) in which one foramen is present on the right side only. The one remaining *M. dimidiata* that could be sampled (86611) has one foramen present bilaterally. Further variation in this feature concerns the number of foramina, with the maximum of three on the right side and four on the left in *M. domestica* (80018). Multiple foramina on at least one side occur in nine of the 14 *M. breviceaudata* (5061, 52730, 63511, 68360, 68361, 76730–33), and 18 of the 26 *M. domestica* (5008, 80016–18, 80020, 80021, 80023, 80025–28, 80030, 80032, 80034–38). Only the left side of one *M. osgoodi* (5242) could be checked and it had one foramen. *Didelphis albiventris* CM 78203 has a small foramen posterodorsal to and directed towards the sphenopalatine foramen, and *Dasyurus maculatus* CM 50842 has one posterior to and directed towards the sphenopalatine foramen. *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press) have no extra foramina in the orbital process of the palatine.

One or more foramina within the orbital process of the palatine at the level of the ethmoidal foramen occur bilaterally in 13 of the 14 *Monodelphis breviceaudata*, all 27 of the *M. domestica*, the one *M. dimidiata* (86611), and the one *M. sp.* (5024) that could be sampled. The sole exception, *M. breviceaudata* (4681), has two foramina on the left side only. Further variation in this feature concerns the number of foramina, with the maximum of five on the right side and three on the left in *M. domestica* (101529). Multiple foramina on at least one side occur in 7 of the 15 *M. breviceaudata* (4681, 5061, 52730, 63510, 63511, 76732, 76733), 14 of the 27 *M. domestica* (5008, 80016–18, 80021, 80025, 80026, 80028, 80030, 80033, 80034, 80037, 101529, 101531), the one *M. dimidiata*, and the one *M. sp.* Only the left side of one *M. osgoodi* (5242) could be checked and it had two foramina. *Didelphis albiventris* CM 78203 has two on the right side and one on the left at the level of the ethmoidal foramen; *Dasyurus maculatus* CM 50842 has none.

A foramen anterodorsal to the previous one considered, near the suture with the frontal occurs bilaterally in all the CM *Monodelphis* specimens that could be sampled: 14 *M. breviceaudata*, 27 *M. domestica*, four *M. dimidiata*, and one *M. sp.* (5024). Only the left side of one *M. osgoodi* (5242) could be checked, and the foramen is present. The only variant is that rather than being situated entirely within the palatine, the foramen is in the suture between the palatine and frontal bilaterally in one *M. breviceaudata* (68359), and on one side

only in one *M. brevicaudata* (76733) and two *M. domestica* (80023, 80032). *Didelphis albiventris* CM 78203 has a similar small foramen within the palatine near the frontal, anterior to the level of the ethmoidal foramen. *Dasyurus maculatus* CM 50842 has a relatively larger aperture within the palatine near the frontal, but it is more anteriorly placed, halfway between the sphenopalatine and ethmoidal foramina.

An elongate, irregular opening in the suture between the palatine and pterygoid occurs in nine of the 15 remaining *Monodelphis brevicaudata*, all 28 *M. domestica*, one of the two *M. dimidiata* (86611), and the one *M. osgoodi* (5242) that could be sampled. A comparable gap is lacking in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press).

Parietal.—*Monodelphis brevicaudata* CM 52729 (Fig. 1) has a small foramen in the left parietal just anterior to the interparietal bone that leads into a posterodorsomedially directed groove on the interparietal bone. This foramen is present on one or both sides in 31 of the 48 remaining CM specimens that could be sampled, the exceptions being seven *M. brevicaudata* (4681, 52730, 63509, 68358, 68361, 76730, 76733), nine *M. domestica* (80017, 80019, 80020, 80030, 80033–35, 80037, 80038), and *M. osgoodi* (5242). A foramen is present bilaterally in three *M. brevicaudata* (68359, 68360, 76734), twelve *M. domestica* (5008, 80016, 80018, 80021, 80025, 80027, 80031, 80032, 80036, 80039, 80040, 101531), three *M. dimidiata* (86608, 86610, 86611), and one *M. osgoodi* (5248). The foramen is lacking in the other *M. osgoodi* (5242), but the condition could not be confirmed in the remaining *M. dimidiata* because the parietals were covered with connective tissue. The foramen is present on one side only in four *M. brevicaudata* (63510, 63511, 76731, 76732) and five *M. domestica* (5010, 80024, 80028, 80029, 101529). There are two unusual cases in *M. domestica*; CM 5025 has three foramina on the left and two on the right, and CM 80023 has one in the right side only, but four in the interparietal on the same side and two in the interparietal on the opposite side.

Didelphis albiventris CM 78203 does not have comparable foramina in the parietal, but does have four tiny foramina in the interparietal to the right of the sagittal crest and one to the left, and two tiny foramina in the interparietal anterior to the right nuchal crest and three anterior to the left. As in some *Monodelphis*, *Dasyurus maculatus* CM 50842 has two foramina per side in the parietal that lead into grooves running posterodorsally. Comparable foramina in the parietal are not reported for *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Zalambdalestes lechei* (Wible et al., in press).

Petrosal.—On the right side of *Monodelphis osgoodi* CM 5242, there is a foramen in the anteromedial flange of the petrosal somewhat larger than the anterior hypoglossal foramen that leads into a shallow sulcus directed anteromedially toward the carotid foramen. This foramen leads into a canal that bends dorsomedially and opens endocranially. In light of the canal's position, its endocranial aperture presumably is within or near the sulcus for the inferior petrosal sinus, and its occupant, therefore, may be venous. On the specimen's left side, a foramen in the anteromedial flange exists without a sulcus, but the foramen is roughly one-quarter the size of that on the right side. No other specimen in the CM sample has a foramen in the anteromedial flange. However, the left side of the second *M. osgoodi* CM 5248 has an aperture filled with dried blood between the anteromedial flange of the petrosal and basisphenoid with a sulcus directed anteromedially toward the carotid foramen. On the right side comparable structures do not exist. Several *M. domestica* (e.g., 80018, 80026) have a similarly placed opening bilaterally present between the anteromedial flange and basisphenoid; Archer (1976:p. 281) described a similar opening in *M. dimidiata* WAM M6785. It seems likely that these openings are functioning like the foramina in the anteromedial flange of *M. osgoodi* CM 5242. Given that the suture between the

anteromedial flange and basisphenoid is not a tight one, it is possible that small venous channels may be present more widely in the CM sample than the osteology suggests.

Comparable openings, either within the anteromedial flange or between that and the basisphenoid, are not present in *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Wible et al., in press).

Premaxilla.—*Monodelphis brevicaudata* CM 52729 (Fig. 2) has a tiny foramen bilaterally present in the facial component of the premaxilla dorsal to the I3–4 embrasure, near the rim of the external nasal aperture. In the remaining *M. brevicaudata*, a similar aperture is either absent bilaterally (4681, 63510, 63511, 68358, 68359 76732, 76733), present on one side only (5061, 52730, 63509, 68360, 68361), or bilaterally present (76730, 76731, 76734). *M. domestica* shows a similar pattern: absent bilaterally (5008, 5010, 80031, 80032, 80034, 80039, 80040, 101529), present on one side only (5025, 80016, 80017, 80019, 80021, 80028–30, 80033, 80038), or bilaterally present (80020, 80023–27, 80035–37, 101531). These foramina are absent in three *M. dimidiata* (86608–10) and present on one side only in the fourth (86611). In the two *M. osgoodi*, foramina are absent in one (5242) and bilaterally present in the other (5248). In the *M. sp.*, the foramina are absent (5002, 5003) or double bilaterally (50024).

Didelphis albiventris CM 78203 has a tiny foramen on the right side only posterodorsal to the I5. *Dasyurus maculatus* CM 50842 has a tiny foramen bilaterally placed dorsal to the I4 and three dorsal to the I5 on the left side only. Similar foramina are not reported for *Pucadelphys andinus* (Marshall and Muizon, 1995) or *Zalambdalestes lechei* (Wible et al., in press).

Squamosal.—*Monodelphis brevicaudata* CM 52729 (Fig. 1) has a triangular depression on the dorsum of the posterior root of the zygoma. In the posterior corner of this depression is a small foramen in the squamosal that communicates with the postglenoid foramen and is hidden in dorsal view by the ridge running along the dorsal edge of the zygoma. One or more foramina are present bilaterally in the remaining 13 *M. brevicaudata*, the 21 *M. domestica*, the one *M. dimidiata* (86609), and the one *M. sp.* (5024) that could be sampled. Two or more foramina are present bilaterally in four *M. brevicaudata* (52730, 63509, 63511, 76730) and seven *M. domestica* (80016, 80017, 80025, 80031, 80032, 80036, 80039). The maximum of four on one side and three on the other occurs in *M. domestica* (80032). Only the left side of one *M. osgoodi* (5042) could be sampled and it had one foramen. *Didelphis albiventris* CM 78203 has three foramina on the right and six on the left; *Dasyurus maculatus* CM 50842 has four on the right and six on the left. None is reported for *Pucadelphys andinus* (Marshall and Muizon, 1995) or *Zalambdalestes lechei* (Wible et al., in press).

Monodelphis brevicaudata CM 52729 (Fig. 4) and the bulk of the CM sample have a small anteriorly directed foramen in the lateral surface of the postglenoid process. This foramen is absent on one side only in two *M. domestica* (80020, 80038). Bilateral double foramina are found in one *M. brevicaudata* (52730). Double foramina on one side and single on the other occur in four *M. domestica* (80016, 80021, 80025, 80040) and one *M. sp.* (50024). Double foramina on one side and triple on the other are found in three *M. brevicaudata* (63509, 63511, 76730). *Didelphis albiventris* CM 78203 and *Pucadelphys andinus* (Marshall and Muizon, 1995) have a similar foramen, whereas *Dasyurus maculatus* CM 50842 has two. *Zalambdalestes lechei* (Wible et al., in press) does not have foramina in a comparable position.

Supraoccipital.—Two sorts of foramina are found on the supraoccipital in the CM sample of *Monodelphis*: foramina on the midline at the base of the nuchal crest and foramina more laterally positioned and generally asymmetrically arranged. *M. brevicaudata* CM 52729

(Fig. 9) has only a small, round opening on the midline at the base of the nuchal crest that contained dried blood and was probably an emissary foramen. Given the uncertainty of the position of the interparietal-supraoccipital suture, it is unknown whether this opening was entirely within the supraoccipital or between the supraoccipital and interparietal. One or more foramina on the midline at the base of the nuchal crest are found in 45 of the remaining 48 CM specimens that could be sampled. The three exceptions, one *M. breviceaudata* (4681) and two *M. domestica* (80034, 80035), do not have a foramen in a comparable position, although the last two have a midline foramen that is located well below the nuchal crest. A single foramen is found in eleven *M. breviceaudata* (52730, 63510, 63511, 68358–61, 76730–32, 76734), 21 *M. domestica* (5010, 5025, 80016, 80017, 80020, 80021, 80024–27, 80029–33, 80036–40, 101531), the four *M. dimidiata* (86608–11), and one *M. osgoodi* (5242). Double foramina are found in two *M. breviceaudata* (63509, 76733), five *M. domestica* (80018, 80019, 80023, 80028, 101529), and one *M. osgoodi* (5248). *Didelphis albiventris* CM 78203 has two foramina on the midline within the supraoccipital. *Dasyurus maculatus* CM 50842 has one on the midline and one off to the right entirely within the supraoccipital. *Pucadelphys andinus* (Marshall and Muizon, 1995) has one on the midline, within the supraoccipital-interparietal suture, and *Zalambdalestes lechei* (Wible et al., in press) has no similar opening.

More laterally positioned foramina are more variable in number and position. As in *Monodelphis breviceaudata* CM 52729 (Fig. 9), more laterally positioned foramina are wholly lacking in three other *M. breviceaudata* (68358, 68359, 76732), six *M. domestica* (5025, 80019, 80033–35, 80039), one of the four *M. dimidiata* (86608), and the two *M. osgoodi* (5242, 5248). The remaining 36 specimens that could be sampled had between a low of one foramen on each side (e.g., *M. breviceaudata* CM 76734) and a high of more than 20 foramina on each side (e.g., *M. breviceaudata* CM 68360). *Didelphis albiventris* CM 78203 has two on the right side and four on the left; *Dasyurus maculatus* CM 50842 has only one on the right side. *Pucadelphys andinus* (Marshall and Muizon, 1995) has one per side, and *Zalambdalestes lechei* (Kielan-Jaworowska, 1984; Wible et al., in press) has numerous small foramina, variable in size and number, near the nuchal crest and somewhat ventral to it.

CONCLUSIONS

Comparisons of the cranial osteology of the CM sample of *Monodelphis* with that of other taxa for the purposes of phylogenetic analysis, as models for interpreting extinct forms, and for standardization of terminology are among the ultimate goals of this contribution. Two sorts of limited comparisons are presented (limited because so few relevant forms have been studied to a comparable level): intrageneric (among four of the 15 species of *Monodelphis* recognized by Gardner, 1993); and with four selected outgroups (the didelphid *Didelphis albiventris*, the dasyurid *Dasyurus maculatus*, the early Paleocene metatherian *Pucadelphys andinus*, and the Late Cretaceous eutherian *Zalambdalestes lechei*).

Intrageneric Comparisons

Four species of *Monodelphis* are represented in the CM collection: *M. breviceaudata*, *M. dimidiata*, *M. domestica*, and *M. osgoodi*. The comparisons that follow are limited for the most part to the named and unnamed cranial foramina that were considered in the Discussions. The caveat is what is unique or unusual among four species may not be when all 15 species recognized by Gardner (1993) and relevant outgroups are examined.

The two specimens of *Monodelphis osgoodi* (the holotype CM 5242 and CM 5248) are the most unique among the CM sample. They are distinguished from the remaining 52 *Monodelphis* specimens by four unique features: (1) rather than a fairly distinct foramen for the greater petrosal nerve, one that is barely distinguishable from the foramen ovale; (2) rather than an infraorbital foramen dorsal to the P3 of the P3-M1 embrasure, one that is dorsal to the M1; (3) rather than a sliver of palatine in the maxillary foramen, a well-developed process that contributes to the medial and dorsal walls of the maxillary foramen; and (4) rather than a foramen through the postpalatine torus, a very shallow notch is present. In addition, they have seven features with a limited distribution among the CM sample: (1) the anterior hypoglossal foramen is larger than the posterior (also in one *M. breviceaudata* and seven *M. domestica*); (2) the posttemporal notch is absent bilaterally (also in a three *M. domestica*); (3) subsquamosal foramina are lacking (also in a three *M. breviceaudata* and three *M. dimidiata*); (4) unnamed foramina in the lacrimal dorsal to the maxillary foramen are lacking (also in one *M. domestica* and one *M. dimidiata*); (5) an unnamed foramen in the maxilla dorsal to the P2 is lacking bilaterally (also in two *M. domestica*, one *M. dimidiata*, and one *M. sp.*); (6) unnamed foramina in the supraoccipital off the midline are lacking (also in three *M. breviceaudata*, six *M. domestica*, and one *M. dimidiata*); and (7) the stapes lacks an intracranial foramen, based on CM 5242 (also in two *M. dimidiata* with the third having a microperforation). In fact, the absence of a well-developed intracranial foramen is unique to *M. osgoodi* and *M. dimidiata* among the CM sample.

Only one other cranial feature is potentially unique to one of the remaining three *Monodelphis* species in the CM sample. A separate, small, midline ossification on the dorsal rim of the foramen magnum may distinguish *M. domestica* from the other species. However, such an element is only known for eleven *M. domestica*. It is uncertain whether this element has fallen out of the remaining 16 *M. domestica* preserving the occiput (or for that matter *M. breviceaudata*, *M. dimidiata*, and *M. osgoodi*) or fails to form altogether. One *M. breviceaudata* (68358) has two small, rod-shaped elements in a comparable location, with the right one twice the size of the left. The four *M. dimidiata* (CM 86608–11) have three features with a limited distribution among the remaining CM sample: (1) an infraorbital foramen situated dorsal to the posterior root of P3 (also in four *M. breviceaudata*, 23 *M. domestica*, and one *M. sp.*), whereas the remaining small *Monodelphis* have the foramen more posteriorly positioned (i.e., *M. osgoodi*); (2) parietal foramina are lacking (also in four *M. breviceaudata* and eight *M. domestica*); and (3) the stapes lacks an intracranial foramen in the three specimens preserving the bone (also in *M. osgoodi* CM 5242).

The cranial foramina considered in the CM sample can be categorized into three groups: (1) foramina bilaterally present in all specimens that exhibit no significant variation (carotid foramen, ethmoidal foramen, foramen for the inferior petrosal sinus, incisive foramen, jugular foramen, major palatine foramen, mandibular foramen, minor palatine foramen, pterygoid canal, sphenopalatine foramen, sphenorbital fissure, stylomastoid notch, and transverse canal foramen); (2) bilateral or midline foramina that are present in all specimens but exhibiting significant variation in size, number, position, distinctness from other foramina, or elements contributing to its walls (foramen for the frontal diploic vein, foramen for the greater petrosal nerve, foramen magnum, foramen ovale, foramen rotundum, hypoglossal foramen, infraorbital foramen, lacrimal foramen, maxillary foramen, postglenoid foramen, postzygomatic foramen, suprameatal foramen, unnamed foramen through the postpalatine torus, unnamed foramen in the orbital process of the palatine in or near the frontal suture, and unnamed foramen in the dorsum of the posterior zygomatic root of the squamosal); and (3) foramina that are not present in all specimens that also vary in size, number, and position (accessory palatine foramen, condyloid canal, parietal foramen,

posttemporal notch, subsquamosal foramen, glaserian fissure in alisphenoid tympanic process for the chorda tympani, unnamed foramen in the orbital process of the lacrimal, unnamed foramen in the facial process of the maxilla dorsal to P2, unnamed foramen in the orbitosphenoid, unnamed foramina in the palatine near the sphenopalatine foramen and at the level of the ethmoidal foramen, unnamed foramen between the palatine and pterygoid, unnamed foramen in the parietal near the interparietal, unnamed foramen in the anteromedial flange of the petrosal, unnamed foramen in the facial process of the premaxilla, unnamed foramen in the lateral surface of the postglenoid process, and unnamed foramina in the supraoccipital). Finally, some foramina on the petrosal were not widely sampled and are requiring of further investigation (hiatus Fallopii, internal acoustic meatus, prootic canal, secondary facial foramen, and sigmoid sinus canal).

Outgroup Comparisons

Following the phylogenetic analysis of Rougier et al. (1998), cranial foramina present in *Monodelphis* and *Didelphis albiventris* might be present in didelphids primitively; in the two didelphids plus *Dasyurus maculatus* might be present in marsupials primitively; in the three marsupials plus *Pucadelphys andinus* might be present in metatherians primitively; and in the four metatherians plus *Zalambdalestes lechei* might be present in therians primitively. The named and unnamed foramina unique to five taxonomic units are listed below: *Monodelphis*, Didelphidae, Marsupialia, Metatheria, and Theria. Following the foramen and its condition in parentheses are the number of CM *Monodelphis* that exhibit the foramen and condition. The caveat is the very small outgroup sample size and the possibility of preservational bias, with the fossils perhaps not preserving the numerous small foramina that are encountered in the extant taxa.

Monodelphis.—Distinguishing CM *Monodelphis* from the outgroups are: (1) a condyloid canal (at least on one side in 37 of 39 CM *Monodelphis*); (2) two lacrimal foramina on the facial process of the lacrimal (in 53 of 54 CM *Monodelphis*); (3) a small foramen in the posteroventral base of the orbitosphenoid (in 31 of 42 CM *Monodelphis*); and (4) a gap between the palatine and pterygoid (in 40 of 47 CM *Monodelphis*).

Didelphidae.—Distinguishing CM *Monodelphis* and *Didelphis albiventris* CM 78203 from the outgroups are: (1) an elongate major palatine foramen largely within the maxilla, but with the palatine forming the posterior border (in all CM *Monodelphis*); (2) a small foramen in the orbital process of the lacrimal dorsal to the maxillary foramen (at least on one side in 47 of 52 CM *Monodelphis*); and (3) one or more foramina in the orbital process of the palatine at the level of the ethmoidal foramen (bilaterally in 42 of 43 CM *Monodelphis*).

Marsupialia.—Distinguishing CM *Monodelphis*, *Didelphis albiventris* CM 78203, and *Dasyurus maculatus* CM 50842 from the outgroups are: (1) small accessory palatine foramina (in 53 of 54 CM *Monodelphis*); (2) an ethmoidal foramen between the frontal and orbitosphenoid (in all CM *Monodelphis* preserving the foramen); (3) two hypoglossal foramina with the anterior smaller than the posterior (in most CM *Monodelphis*); (4) two lacrimal foramina with at least one on the facial process of the lacrimal (in 53 of 54 CM *Monodelphis*); (5) a parietal foramen (in 34 of 50 CM *Monodelphis*); (6) postzygomatic foramina (in most CM *Monodelphis*); (7) a sphenorbital fissure formed at least by the alisphenoid, orbitosphenoid, palatine, and presphenoid (in all CM *Monodelphis* preserving the fissure); (8) small subsquamosal foramen in the squamosal (in 43 of 49 CM *Monodelphis*); (9) a transverse canal foramen (in all CM *Monodelphis* preserving the foramen); (10) a glaserian fissure in the alisphenoid tympanic process (in all CM *Monodelphis* preserving the alisphenoid tympanic process); (11) a small foramen in the

maxilla dorsal to the premolars or first molar at least on one side (in 49 of 54 CM *Monodelphis*); (12) a small foramen in the palatine posterior to the sphenopalatine foramen (in 39 of 42 CM *Monodelphis*); (13) a small foramen in the palatine (or between the palatine and frontal) anterior to the ethmoidal foramen (in all CM *Monodelphis* preserving the right and left palatine); (14) a small foramen in the facial process of the premaxilla, near the external nasal aperture, at least on one side (in 23 of 44 CM *Monodelphis*); and (15) a small foramen in the dorsal surface of the squamosal at the posterior root of the zygoma (in all CM *Monodelphis* preserving this part of the squamosal).

Metatheria.—Distinguishing CM *Monodelphis*, *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, and *Pucadelphys andinus* (Marshall and Muizon, 1995) from the outgroup are: (1) a partial or complete foramen for the greater petrosal nerve (in all CM *Monodelphis* preserving the region); (2) a separate foramen for the inferior petrosal sinus (in all CM *Monodelphis* preserving the region); (3) an elongate incisive foramen largely in the premaxilla, but with the maxilla forming the posterior border (in all CM *Monodelphis* preserving the region); (4) a maxillary foramen between the lacrimal, maxilla, and palatine (in all CM *Monodelphis* preserving the region); (5) a narrow, horizontal prootic canal (in all CM *Monodelphis* preserving the region); (6) a secondary facial foramen well anterior to the fenestra vestibuli (in all CM *Monodelphis* preserving the region) (condition not known for *D. maculatus* CM 50842); (7) a sphenopalatine foramen within the palatine (in all CM *Monodelphis* preserving the region); (8) a foramen on the midline posteroventral to the nuchal crest (in 45 of 48 CM *Monodelphis*); and (9) a sphenorbital fissure that transmits the optic nerve (an exception within Metatheria has been reported recently in Late Cretaceous *Deltatheridium* by Rougier et al., in press).

Theria.—Present in CM *Monodelphis*, *Didelphis albiventris* CM 78203, *Dasyurus maculatus* CM 50842, *Pucadelphys andinus* (Marshall and Muizon, 1995), and *Zalambdalestes lechei* (Kielan-Jaworowska and Trofimov, 1981; Kielan-Jaworowska, 1984; Wible et al., in press) are: (1) a carotid foramen in the basisphenoid (in all CM *Monodelphis* preserving the region); (2) a foramen rotundum with the anterior aperture separate from the sphenorbital fissure (in all CM *Monodelphis* preserving the region); (3) a minor palatine foramen between the palatine and maxilla with a thin posterior bridge (in all CM *Monodelphis* preserving the region); (4) a postglenoid foramen in the squamosal (in all CM *Monodelphis* preserving the region); (5) a posttemporal notch or foramen (at least on one side in all CM *M. brevicaudata* and *M. domestica* preserving the region); (6) a suprameatal foramen (in all CM *Monodelphis* preserving the region); and (7) small foramina in the supraoccipital ventral to the nuchal crest (in 35 of 44 CM *Monodelphis*). *Z. lechei* differs from the remaining taxa in two features for which other basal eutherians present the metatherian condition: (1) a foramen for the frontal diploic vein (at least on one side in all CM *Monodelphis* preserving the region and in the zalambdalestid *Kulbeckia kulbecke*, Archibald and Averianov, 2003); and (2) a mandibular foramen just dorsal to the anterior root of the mandibular angle (in all CM *Monodelphis* preserving the region and in *Prokennalestes*, Kielan-Jaworowska and Dashzeveg, 1989).

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APPENDIX 1

Monodelphis specimens examined; all CM numbers.

Monodelphis breviceaudata—Brazil: female 5061; male 4681. Suriname: female 52729, 63510, 63511, 68358, 68359, 68360, 68361; male 52730, 63509, 76730, 76731, 76732, 76733, 76734.

Monodelphis dimidiata—Argentina: female 86608, 86609, 86610; male 86611.

Monodelphis domestica—Bolivia: female 5008, 5025; male 5010. Brazil: female 80017, 80018, 80019, 80025, 80028, 80030, 80031, 80033, 80034, 80038, 80040, 101531; male 80016, 80020, 80021, 80023, 80024, 80026, 80027, 80029, 80032, 80035, 80036, 80037, 80039, 101529.

Monodelphis osgoodi—Bolivia: male 5242, 5248.

Monodelphis sp.—Bolivia: female 5002, 5003, 5024.

APPENDIX 2

Cranial measurements (mm) of *Monodelphis*; all CM numbers. Length of mandible was taken from the anterior tip of the bone to the condylar process. * = estimated measurement. ^a Specimen retaining the upper and lower deciduous third premolars and the M3 and m4 in crypts. ^b Specimen retaining the upper and lower deciduous third premolars with the M3 in a crypt and the m4 erupting. ^c Specimen retaining the upper and lower deciduous third premolars with the M3 erupting and the m4 erupted. ^d Specimen retaining the upper and lower deciduous third premolars with the M4 in a crypt. ^e Specimen retaining the lower deciduous third premolar and the M4 erupting.

	Premaxillary-Condylar Length	Greatest Zygomatic Breadth	Length of Mandible
<i>M. breviceaudata</i>			
4681	36.9	19.5	27.4
5061	—	19.5	26.7
52729	34.7	18.5	25.7
52730	35.4	20.0	25.7
63509	32.7	17.1*	24.4
63510	31.2	16.7	22.8
63511	—	17.5	25.3
68358	36.2	19.4	26.6
68359	36.3	18.9	26.8
68360 ^c	17.2	14.7	17.6
68361	33.4	17.3	24.2
76730	35.7	18.8	26.1
76731	35.5	18.4	26.5
76732	38.7	20.8	28.7
76733 ^d	30.6	16.5	22.4
76734 ^b	28.6	15.2	20.3

APPENDIX 2

Continued.

	Premaxillary-Condylar Length	Greatest Zygomatic Breadth	Length of Mandible
<i>M. dimidiata</i>			
86608	24.3	12.3	17.1
86609	29.7	15.7	21.4
86610	24.8	12.2	17.2
86611	24.8	12.2	16.4
<i>M. domestica</i>			
5008	—	19.4	25.7
5010	38.6	21.5	29.2
5025	—	—	24.7
80016	44.7	24.3	34.4
80017	41.9	21.7	31.3
80018	39.6	20.1	29.0
80019 ^b	29.7	15.6	21.1
80020 ^a	28.2	15.3	20.4
80021	40.6	21.4	30.4
80023	43.7	23.5	33.0
80024	37.8	20.2	28.3
80025	40.4	22.3	30.7
80026	38.2	20.7	28.7
80027	39.5	21.1	29.7
80028	40.6	22.2	31.1
80029	44.0	25.0	34.0
80030	40.2	22.1	30.3
80031	39.6	21.8	30.4
80032	36.9	19.6	27.9
80033 ^b	31.9	16.9	22.7
80034	37.2	19.0	27.2
80035 ^a	26.7	14.3	19.0
80036	41.6	23.5	30.9
80037	43.4	22.7	32.1
80038	41.3	22.2	30.8
80039 ^c	35.7	18.3	27.5
80040	42.8	23.5	32.5
101531	38.8	20.4	29.3
101529	42.4	23.0	32.4
<i>M. osgoodi</i>			
5242	25.8	12.4	17.2
5248	25.4	11.8	18.1
<i>Monodelphis</i> sp.			
5002	—	—	23.5*
5003 ^d	—	—	20.6*
5024	—	20.1	26.8

APPENDIX 3

List of Anatomical Terms: On the left are the terms used here; on the right are references and/or Nomina Anatomica Veterinaria (NAV) equivalents.

Abducens Nerve	Nervus abducens (NAV)
Accessory Palatine Artery	(Evans, 1993)
Accessory Palatine Foramen	(Wible and Rougier, 2000); Minor Palatine Foramen (Evans, 1993)
Accessory Palatine Nerve	Nervus palatinus accessorius (NAV)
Ala of Vomer	Ala vomeris (NAV)
Alisphenoid	Os basisphenoidale, Ala (NAV)
Angular Process	Processus angularis (NAV)
Anterior Nasal Notch	(Lillegraven and Krusat, 1991)
Anterior Process of Alisphenoid	(Wible et al., in press)
Anterior Process of Malleus	(De Beer, 1937)
Anteromedial Flange of Petrosal	(Wible et al., in press); Periotic Hypotympanic Sinus (Archer, 1976)
Aqueductus vestibuli	(NAV)
Arteria anastomotica	(Wible, 1987)
Arteria diploëtica magna	(Wible, 1987)
Artery of Pterygoid Canal	(Evans, 1993)
Auditory Tube	Tuba auditiva (NAV)
Basilar Sinus	Sinus basilaris (NAV)
Basioccipital	Os occipitale, Pars basilaris (NAV)
Basisphenoid	Os basisphenoidale, Corpus (NAV)
Body of Mandible	Corpus mandibulae (NAV)
Canal for Sigmoid Sinus	New Term
Capsuloparietal Emissary Vein	(Gelderen, 1924)
Carotid Foramen	Canalis caroticus (NAV)
Carotid Sulcus	Sulcus caroticus (NAV)
Caudal Nasal Artery	Arteriae nasales caudales (NAV)
Caudal Nasal Nerve	Nervus nasalis caudalis (NAV)
Caudal Palatine Foramen	(Evans, 1993)
Caudal Tympanic Process of Petrosal	(MacPhee, 1981)
Cavernous Sinus	Sinus cavernosus (NAV)
Cavum epiptericum	(Gaupp, 1902, 1905; De Beer, 1937)
Cavum supracochleare	(Voit, 1909; De Beer, 1937)
Choanae	(NAV)
Chorda Tympani Nerve	Chorda tympani (NAV)
Cochlear Canaliculus	Canaliculus cochleae (NAV)
Cochlear Duct	Ductus cochlearis (NAV)
Cochlear Fossula	(MacPhee, 1981)
Cochlear Nerve	Nervus cochlearis (NAV)
Condylar Process	Processus condylaris (NAV)
Condylod Canal	Canalis condylaris (NAV)
Condylod Vein	(Evans, 1993)
Coronoid Crest	(Evans, 1993)
Coronoid Process	Processus coronoideus (NAV)
Cranial Accessory Nerve	Radices spinales, Nervus accessorius (NAV)
Crista Parotica	(De Beer, 1937)
Crista Petrosa	(Wible, 1990)
Crus breve, Incus	(NAV)
Crus Commune	(Wible, 1990)
Digastric Muscle	Musculus digastricus (NAV)
Ectotympanic	Os temporale, pars tympanica (NAV)
Element of Paaw	(Klaauw, 1923; De Beer, 1937)
Endolymphatic Duct	Ductus endolymphaticus (NAV)
Entopterygoid Crest	(Novacek, 1986)
Epitympanic Recess	Recessus epitympanicus (NAV)
Ethmoid	Os ethmoidale (NAV)

Ethmoidal Foramen	Foramen ethmoidale (NAV)
Ethmoidal Nerve	Nervus ethmoidalis (NAV)
Exoccipital	Os occipitale, Pars lateralis (NAV)
External Acoustic Meatus	Meatus acusticus externus (NAV)
External Jugular Vein	Vena jugularis externa (NAV)
External Nasal Aperture	Apertura nasi osseum (NAV)
External Occipital Protuberance	Protuberantia occipitalis externa (NAV)
Facial Nerve	Nervus facialis (NAV)
Facial Process of Lacrimal	Os lacrimale, Facies facialis (NAV)
Facial Process of Maxilla	Maxillare, Facies facialis (NAV)
Facial Process of Premaxilla	Os incisivum, Facies labialis (NAV)
Facial Sulcus	(MacPhee, 1981)
Fenestra cochleae	(NAV)
Fenestra vestibuli	(NAV)
Foramen acusticum inferius	Ventral Vestibular Area (Evans, 1993)
Foramen acusticum superius	Facial Canal + Dorsal Vestibular Area (Evans, 1993)
Foramen for Frontal Diploic Vein	(Thewissen, 1989)
Foramen for Inferior Petrosal Sinus	(Wible, 1983)
Foramen magnum	(NAV)
Foramen ovale	(NAV)
Foramen rotundum	(NAV)
Foramen singulare	(NAV)
Fossa for Stapedius Muscle	(MacPhee, 1981)
Fossa for Tensor Tympani Muscle	(MacPhee, 1981)
Fossa incudis	(MacPhee, 1981)
Frontal	Os frontale (NAV)
Frontal Diploic Vein	Vena diploica frontalis (NAV)
Frontal Process of Jugal	Os zygomaticum, Processus frontalis (NAV)
Geniculate Ganglion	Ganglion geniculi (NAV)
Glaserian Fissure	Fissura Glaseri (Klaauw, 1931)
Glenoid Fossa	Fossa mandibularis (NAV)
Glenoid Process of Jugal	(Rougier et al., 1998; Wible et al., in press)
Glossopharyngeal Nerve	Nervus glossopharyngeus (NAV)
Greater Petrosal Nerve	Nervus petrosus major (NAV)
Hamulus	Hamulus pterygoideus (NAV)
Hiatus Fallopii	Petrosal Canal (Evans, 1993)
Horizontal Process of Palatine	Os palatinum, Lamina horizontalis (NAV)
Hypoglossal Foramen	Canalis nervus hypoglossi (NAV)
Hypoglossal Nerve	Nervus hypoglossus (NAV)
Hypophysis	(NAV)
Hypotympanic Sinus of Alisphenoid	(Archer, 1976)
Incisive Foramen	Fissura palatina (NAV)
Incus	(NAV)
Inferior Alveolar Nerve	Nervus alveolaris inferior (NAV)
Inferior Petrosal Sinus	Sinus petrosus ventralis (NAV)
Infraorbital Artery	Arteria infraorbitalis (NAV)
Infraorbital Canal	Canalis infraorbitale (NAV)
Infraorbital Foramen	Foramen infraorbitale (NAV)
Infraorbital Margin	Margo infraorbitalis (NAV)
Infraorbital Nerve	Nervus infraorbitalis (NAV)
Infraorbital Vein	Vena infraorbitalis (NAV)
Infratemporal Crest	Crista infratemporalis (NAV)
Infratemporal Fossa	Fossa infratemporalis (NAV)
Internal Acoustic Meatus	Meatus acusticus internus (NAV)
Internal Carotid Artery	Arteria carotis interna (NAV)
Internal Carotid Nerve	Nervus caroticus interna (NAV)
Internal Jugular Vein	Vena jugularis interna (NAV)
Interparietal	Os interparietalis (NAV)
Intracranial Foramen of Stapes	Foramen intracraniale (Fleischer, 1973)
Jugal	Os zygomaticum (NAV)

Jugular Foramen	Foramen jugulare (NAV)
Lacrimal	Os lacrimale (NAV)
Lacrimal Canaliculus	Canaliculus lacrimalis (NAV)
Lacrimal Foramen	Foramen lacrimale (NAV)
Lacrimal Sac	Saccus lacrimalis (NAV)
Lateral Head Vein	(Wible, 1990; Wible and Hopson, 1993; Rougier and Wible, in press)
Lateral Pterygoid Muscle	Musculus pterygoideus lateralis (NAV)
Levator Labii Muscle	Musculus levator labii superioris (NAV)
Longus Capitis Muscle	Musculus longus capitis (NAV)
Major Palatine Artery	Arteria palatina major (NAV)
Major Palatine Foramen	Foramen palatinum majus (NAV)
Major Palatine Nerve	Nervus palatinus major (NAV)
Malleus	(NAV)
Mandible	Mandibula (NAV)
Mandibular Foramen	Foramen mandibulae (NAV)
Mandibular Nerve	Nervus mandibularis (NAV)
Mandibular Notch	(Evans, 1993); Incisura mandibulae (NAV)
Mandibular Symphysis	(Evans, 1993)
Masseter Muscle	Musculus masseter (NAV)
Masseteric Fossa	Fossa masseterica (NAV)
Masseteric Line	(Evans, 1993)
Mastoid Exposure	Mastoid Process (Evans, 1993)
Mastoid Process	Processus mastoideus (NAV)
Maxilla	(NAV)
Maxillary Artery	Arteria maxillaris (NAV)
Maxillary Foramen	Foramen maxillare (NAV)
Maxillary Nerve	Nervus maxillaris (NAV)
Maxilloturbinal	Os conchae nasalis ventralis (NAV)
Medial Pterygoid Muscle	Musculus pterygoideus medialis (NAV)
Mental Foramen	Foramen mentale (NAV)
Minor Palatine Artery	Arteria palatina minor (NAV)
Minor Palatine Foramen	Foramen palatinum caudale (NAV)
Minor Palatine Nerve	Nervus palatinus minor (NAV)
Mylohyoid Line	Linea mylohyoideus (NAV)
Mylohyoid Muscle	Musculus mylohyoideus (NAV)
Mylohyoid Nerve	Nervus mylohyoideus (NAV)
Nasal	Os nasale (NAV)
Nasal Fossa	Cavum nasi (NAV)
Nasal Septum	Septum nasi osseum (NAV)
Nasolacrimal Canal	Canalis nasolacrimalis (NAV)
Nasolacrimal Duct	Ductus nasolacrimalis (NAV)
Nasopalatine Duct	(Cooper and Bhatnagar, 1976); Ductus incisivus (NAV)
Nasopharyngeal Passage	Meatus nasopharyngeus (NAV)
Nerve of Pterygoid Canal	Nervus canalis pterygoidei (NAV)
Nuchal Crest	Crista nuchae (NAV)
Occipital Condyle	Condylus occipitalis (NAV)
Oculomotor Nerve	Nervus oculomotorius (NAV)
Odontoid Notch	Intercondyloid Notch (Evans, 1993)
Ophthalmic Artery	Arteria ophthalmica interna (NAV)
Ophthalmic Nerve	Nervus ophthalmica (NAV)
Ophthalmic Vein	Vena ophthalmica interna (NAV)
Optic Foramen	Canalis opticus (NAV)
Optic Nerve	Nervus opticus (NAV)
Orbital Fossa	Orbita (NAV)
Orbital Process of Lacrimal	Os lacrimale, Facies orbitalis (NAV)
Orbital Process of Maxilla	Maxillare, Facies orbitalis (NAV)
Orbitosphenoid	Os presphenoidale, Ala (NAV)
Orbitotemporal Crest	Crista orbitotemporalis (NAV)
Orbitotemporal Fossa	Orbita + Fossa temporalis (NAV)

Palatal Process of Maxilla	Maxillare, Processes palatinus (NAV)
Palatal Process of Premaxilla	Os incisivum, Processus palatinus (NAV)
Palatine	Os palatinum (NAV)
Paracondylar Process of Exoccipital	Processus paracondylaris (NAV)
Paraflocculus of Cerebellum	Paraflocculus (NAV)
Parietal	Os parietale (NAV)
Parietal Foramen	(Boyd, 1930, 1934)
Pars canalicularis of Petrosal	(Wible, 1990; Wible et al., 1995, 2001)
Pars cochlearis of Petrosal	(Wible, 1990; Wible et al., 1995, 2001)
Perilymphatic Duct	Ductus perilymphaticus (NAV)
Perpendicular Process of Palatine	Os palatinum, Lamina perpendicularis (NAV)
Petrosal	Os temporale, Pars petrosa (NAV)
Piriform Fenestra	Pyriform Fenestra (McDowell, 1958); Foramen lacerum (NAV)
Posterior Auricular Artery	Arteria auricularis caudalis (NAV)
Posterior Semicircular Canal	Canalis semicircularis posterior (NAV)
Posterior Shelf of Masseteric Fossa	(Marshall and Muizon, 1995)
Posterodorsal Process of Premaxilla	(Wible and Rougier, 2000)
Postglenoid Artery	(Archer, 1976)
Postglenoid Foramen	Foramen retroarticulare (NAV)
Postglenoid Process	Processus retroarticulare (NAV)
Postglenoid Vein	Vena emissaria foraminis retroarticularis (NAV)
Postorbital Ligament	Ligamentum orbitale (NAV)
Postorbital Process	Os frontale, Processus zygomaticus (NAV)
Postpalatine Torus	(Novacek, 1986)
Post-Promontorial Tympanic Sinus	(Wible, 1990); Mastoid Epitympanic Sinus (Archer, 1976)
Posttemporal Foramen (Notch)	(Rougier et al., 1992)
Post-Trigeminal Vein	(Wible and Hopson, 1995; Rougier and Wible, in press)
Posttympenic Crest	(Wible et al., in press)
Posttympenic Process	(Kielan-Jaworowska, 1981; Novacek, 1986); Processus retrotympanicus (NAV)
Postzygomatic Foramen	(Gregory, 1910)
Prefacial Commissure	(De Beer, 1937)
Premaxilla	Os incisivum (NAV)
Presphenoid	Os presphenoidale, Corpus (NAV)
Primary Facial Foramen	(Wible, 1990; Wible and Hopson, 1993)
Promontorium of Petrosal	(Evans, 1993)
Prootic Canal	(Wible, 1990; Rougier and Wible, in press)
Prootic Sinus	(Wible, 1990; Rougier and Wible, in press)
Pterygoid	Os pterygoideum (NAV)
Pterygoid Canal	Canalis pterygoideus (NAV)
Ramus Infraorbitalis	(Wible, 1987)
Ramus of Mandible	Ramus mandibulae (NAV)
Ramus Temporalis of Stapedial Artery	(Wible, 1987)
Rectus Capitis Muscle	Musculus rectus capitis ventralis (NAV)
Rostral Tympanic Process of Petrosal	(Wible, 1990; Sánchez-Villagra and Wible, 2002)
Sacculae	Sacculus (NAV)
Sagittal Crest	Crista sagittalis externa (NAV)
Secondary Facial Foramen	(Wible, 1990; Wible and Hopson, 1993)
Secondary Tympanic Membrane	Membrana tympani secundaria (NAV)
Semicircular Canal	Canalis semicircularis (NAV)
Sigmoid Sinus	Sinus sigmoideus (NAV)
Sphenorbital Fissure	(Gregory, 1910); Fissura orbitalis + Canalis opticus (NAV)
Sphenopalatine Artery	Arteria sphenopalatina (NAV)
Sphenopalatine Foramen	Foramen sphenopalatinum (NAV)
Sphenopalatine Vein	Vena sphenopalatina (NAV)

Sphenoparietal Emissary Vein	(Gelderen, 1924)
Spinal Accessory Nerve	Radices spinales, Nervus accessorius (NAV)
Squamosal	Os temporale, pars squamosa (NAV)
Stapedius Muscle	Musculus stapedius (NAV)
Stapes	(NAV)
Stylohyal	Stylohyoideum (NAV)
Stylomastoid Artery	Arteria stylomastoidea (NAV)
Stylomastoid Notch	Foramen stylomastoideum (NAV)
Subarcuate Fossa	Fossa subarcuata (NAV)
Subsquamosal Foramen	(Wible et al., in press)
Sulcus for Inferior Petrosal Sinus	Sulcus sinus petrosa ventralis (NAV)
Sulcus for Prootic Sinus	(Wible, 1990; Wible and Hopson, 1995)
Sulcus for Sigmoid Sinus	(Wible, 1990; Wible and Hopson, 1995)
Sulcus for Sphenoparietal Emissary Vein	(Wible, 1990; Wible and Hopson, 1995)
Sulcus for Superior Petrosal Sinus	Sulcus sinus petrosa dorsalis (NAV)
Sulcus tympanicus	(NAV)
Suprameatal Foramen	(Novacek, 1986)
Supraorbital Margin	Margo supraorbitalis (NAV)
Superior Orbital Fissure	Fissura orbitalis (NAV)
Superior Petrosal Sinus	Sinus petrosus dorsalis (NAV)
Suprameatal Bridge	Dorsal Boundary of External Acoustic Meatus (Evans, 1993)
Supraoccipital	Squama occipitalis (NAV)
Temporal Fossa	Fossa temporalis (NAV)
Temporal Line	Linea temporalis (NAV)
Temporalis Muscle	Musculus temporalis (NAV)
Temporomandibular Joint	Articulatio temporomandibularis (NAV)
Tensor Tympani Muscle	Musculus tensor tympani (NAV)
Tentorium Cerebelli	Tentorium cerebelli membranaceum (NAV)
Tractus spiralis foraminosus	(NAV)
Transverse Canal Foramen	(Sánchez-Villagra and Wible, 2002)
Transverse Crest of Petrosal	Crista transversa (NAV)
Transverse Frontal Sinus	(Archer, 1976)
Transverse Sinus	Sinus transversus (NAV)
Trigeminal Nerve	Nervus trigeminus (NAV)
Trochlear Nerve	Nervus trochlearis (NAV)
Tuberculum tympani	(Toeplitz, 1920)
Tympanic Process of Alisphenoid	(MacPhee, 1981)
Tympanohyal	Tympanohyoideum (NAV)
Tympanum	(NAV)
Utricle	Utriculus (NAV)
Vagus Nerve	Nervus vagus (NAV)
Vein of Prootic Canal	(Rougier and Wible, in press)
Ventral Condylod Fossa	Fossa condylaris ventralis (NAV)
Vermis of Cerebellum	Vermis (NAV)
Vertebral Artery	Arteria vertebralis (NAV)
Vestibular Fossula	(MacPhee, 1981)
Vestibular Nerve	Nervus vestibularis (NAV)
Vestibulocochlear Nerve	Nervus vestibulocochlearis (NAV)
Vomer	(NAV)
Vomeronasal Organ	Organum vomeronasale (NAV)
Zygoma	Arcus zygomaticus (NAV)
Zygomatic Process of Lacrimal	(Kermack et al., 1981)
Zygomatic Process of Maxilla	Maxillare, Processus zygomaticus (NAV)
Zygomatic Process of Squamosal	Os temporale, Pars squama, Processus zygomaticus (NAV)
Zygomaticomandibularis Muscle	(Turnbull, 1970)
Zygomaticus Muscle	Musculus zygomaticus (NAV)

RODENTS OF THE FAMILY ANOMALURIDAE (MAMMALIA)
FROM SOUTHEAST ASIA (MIDDLE EOCENE,
PONDAUNG FORMATION, MYANMAR)

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ABSTRACT

Latest middle Eocene deposits in the Pondaung Formation of Myanmar have yielded specimens representing the rodent family Anomaluridae. This is the geologically oldest record of the family. There appear to be two or three species of Pondaung anomalurids, the most completely represented taxon of which is described as a new genus and species, *Pondaungimys anomaluropis*. The anomalurids from the Pondaung Formation are characterized by a complex folding pattern on the occlusal surfaces of the cheek teeth, as well as the basically anomalurid pentalophodont condition. Undescribed anomalurids have been reported from the late Eocene of Thailand and Oligocene of Pakistan and the Arabian Peninsula. Their Neogene distribution is only African. This occurrence in the Pondaung Formation adds new evidence to previously reported similarities between Southeast Asian and North African Paleogene mammalian faunas.

KEY WORDS: Rodentia, Anomaluridae, *Pondaungimys*, Middle Eocene, Myanmar

INTRODUCTION

The richly fossiliferous Pondaung Formation of Myanmar has long been known for its record of middle Eocene terrestrial mammals (Pilgrim and Cotter, 1916; Tsubamoto et al., 2000, 2002), including a diversity of Primates, Perissodactyla, and Artiodactyla. Along with the more recently discovered late Eocene fauna from the Krabi Basin of Thailand (Chaimanee et al., 1997; Ducrocq et al., 1997), the Pondaung fauna provides an important record of Paleogene evolutionary and paleogeographic events in southeastern Asia. Increasingly, these faunas show some interesting similarities with others from the Paleogene of northern Africa (Ducrocq et al., 2000).

Recently field teams from Kyoto University and the Myanmar Government have discovered the rodent specimens that are the subject of this report. While rodents have been mentioned in faunal lists from the Pondaung Formation, previously these specimens were not examined in detail and were given only a questionable familial assignment of

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Phiomysidae indet. (Tsubamoto et al., 2000). They provide evidence for an additional instance of faunal affinities between Southeast Asian and African faunas, representing as they do two or three species referable to the family Anomaluridae, a family that has been endemic to Africa throughout the Neogene. The three extant genera of anomalurids, *Anomalurus*, *Zenkerella*, and *Idiurus*, live in central and western Africa.

The Paleogene fossil record of the anomalurids is sparse. The first to be described, and previously geologically oldest, was *Nementchamys lavocati* from the late middle or late Eocene Bir El Ater (or Nementcha) locality of Algeria (Jaeger et al., 1985). Other reports of anomalurids from the Paleogene of Asia include recognition of the family in the Krabi mine of Thailand, 40 meters above the main lignite seam (Ducrocq et al., 1997) and in the Oligocene of Oman (Thomas et al., 1999). In Baluchistan, anomalurids have been reported from the Oligocene of the Bugti Hills (Welcomme et al., 2001). Presence of a fragment of an anomalurid bone in the upper levels of the Fayum has been mentioned (Lavocat, 1973), although this occurrence has not been authenticated by a description.

Terminology and Abbreviations

Dental terminology follows Jaeger et al., 1985.

NMMP: National Museum, Myanmar, Paleontology.

KU: Kyoto University of Japan.

Geologic Setting

The Pondaung Formation is distributed in the western part of central Myanmar (Fig. 1). It overlies and partially interfingers with the Tabyin Formation and is conformably overlain by the Yaw Formation (Stamp, 1922; Bender, 1983; Aye Ko Aung, 1999). The Tabyin Formation consists mainly of marine claystones, yielding *Nummulites acutus*, a benthic foraminifera indicative of the middle Eocene (Eames, 1951; Bender, 1983); whereas the Yaw Formation is mainly composed of marine shales and yields benthic foraminifera (e.g., *Nummulites yawensis*, *Discocyclina sella*, and *Operculina* sp. cf. *O. canalifera*) and molluscs (e.g., *Velates perversus*), both of which indicate the late Eocene (Bender, 1983).

The Pondaung Formation was re-defined as the freshwater deposits of the Pondaung Sandstones (Cotter, 1914) by Aye Ko Aung (1999). The Pondaung Formation (about 2000 m in thickness) consists of alternating mudstone, sandstone, and conglomerate, and is subdivided into the "Lower" and "Upper" Members (Aye Ko Aung, 1999). The "Lower Member" (about 1500 m in thickness) is dominated by greenish pebbly sandstone and mudstone and contains a few fragments of leaf fossils in its upper part (Aye Ko Aung, 1999). The "Upper Member" (about 500 m in thickness) is dominated by fine- to medium-grained sandstone and variegated mudstone (Aye Ko Aung, 1999; Aung Naing Soe, 1999; Aung Naing Soe et al., 2002) and contains many terrestrial mammalian and other vertebrate fossils (e.g., Pilgrim and Cotter, 1916; Pilgrim, 1925, 1927, 1928; Colbert, 1937, 1938; Bender, 1983; Tsubamoto et al., 2000). The mammalian fauna suggests a Bartonian Age (late middle Eocene) for the "Upper Member" (e.g., Holroyd and Ciochon, 1994, 1995). The fission-track age of the "Upper Member" has been calibrated as 37.2 ± 1.3 Ma (= around middle-late Eocene boundary) (Tsubamoto et al., 2002). Therefore, the age of the "Upper Member" is likely to be the latest middle Eocene.

Most mammalian fossils from the Pondaung Formation have been recovered from the lower half of the "Upper Member" (Aye Ko Aung, 2001). The currently known fossil sites for the Pondaung fauna are distributed on the west side of the Chindwin River, extending about 50 km from northwest to southeast, and are roughly divided into three main areas, that is, Bahin, Pangan, and Mogaung (Fig. 1; Tsubamoto et al., 2000).

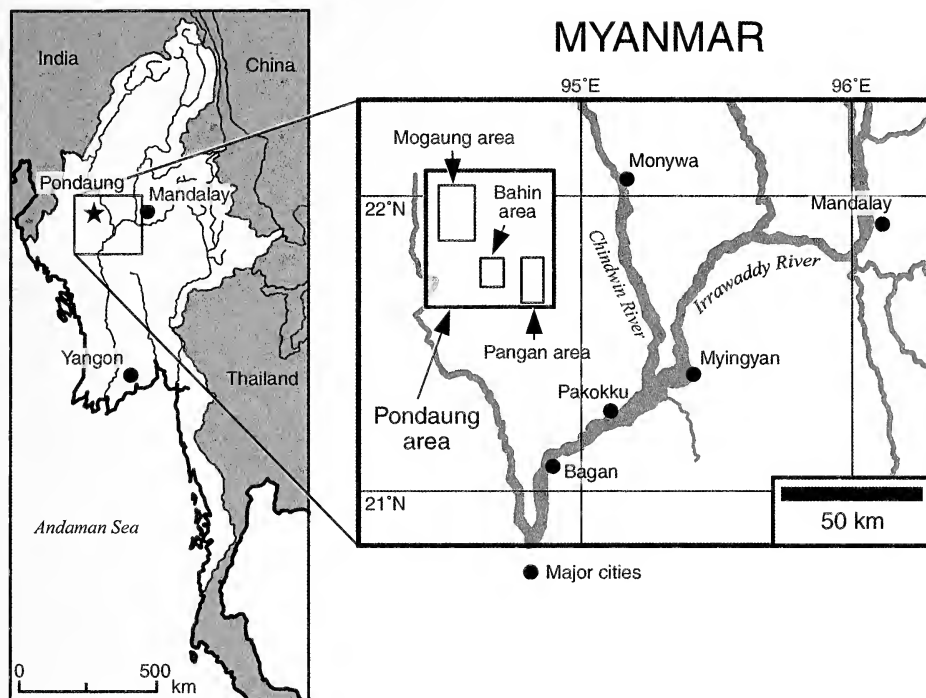


Fig. 1.—Left. Map of part of Southeast Asia showing the location of the Pondaung area within Myanmar. Right. Pondaung area showing localities where the rodent fossils were collected.

SYSTEMATIC PALEONTOLOGY

Family Anomaluridae

Pondaungimys anomaluopsis, new genus and species

Fig. 2

Synonymy: ?Phiomyidae indet. C in Tsubamoto et al., 2000, p. 38–39, Plate 1, A–C.

Holotype.—NMMP-KU 0213, a left mandibular fragment with M_{1-3} .

Repository.—National Museum, Yangon, Myanmar.

Locality.—Bh1 locality, Bahin area (Fig. 1; Tsubamoto et al., 2000, fig. 5).

Formation and Age.—Lower part of the “Upper Member” of the Pondaung Formation; latest middle Eocene.

Diagnosis.—Anomalurid with molars increasing in length from M_1 – M_3 , more lophate than cusate; lower molars having elevated cingula around lingual side and pentalophodont occlusal pattern composed of an anterolophid, metalophulid I, mesolophid, hypolophid, and posterolophid. Metalophulid I and mesolophid complexly branching. Compared to *Nementchamys*, *Pondaungimys* has a less well-developed metalophulid I and fewer small complex folds in the trigonid and central basins. Differs from known Neogene anomalurids in having weaker crests in the occlusal pattern and more complex crenulations.

Dental Measurements.—See Table 1.

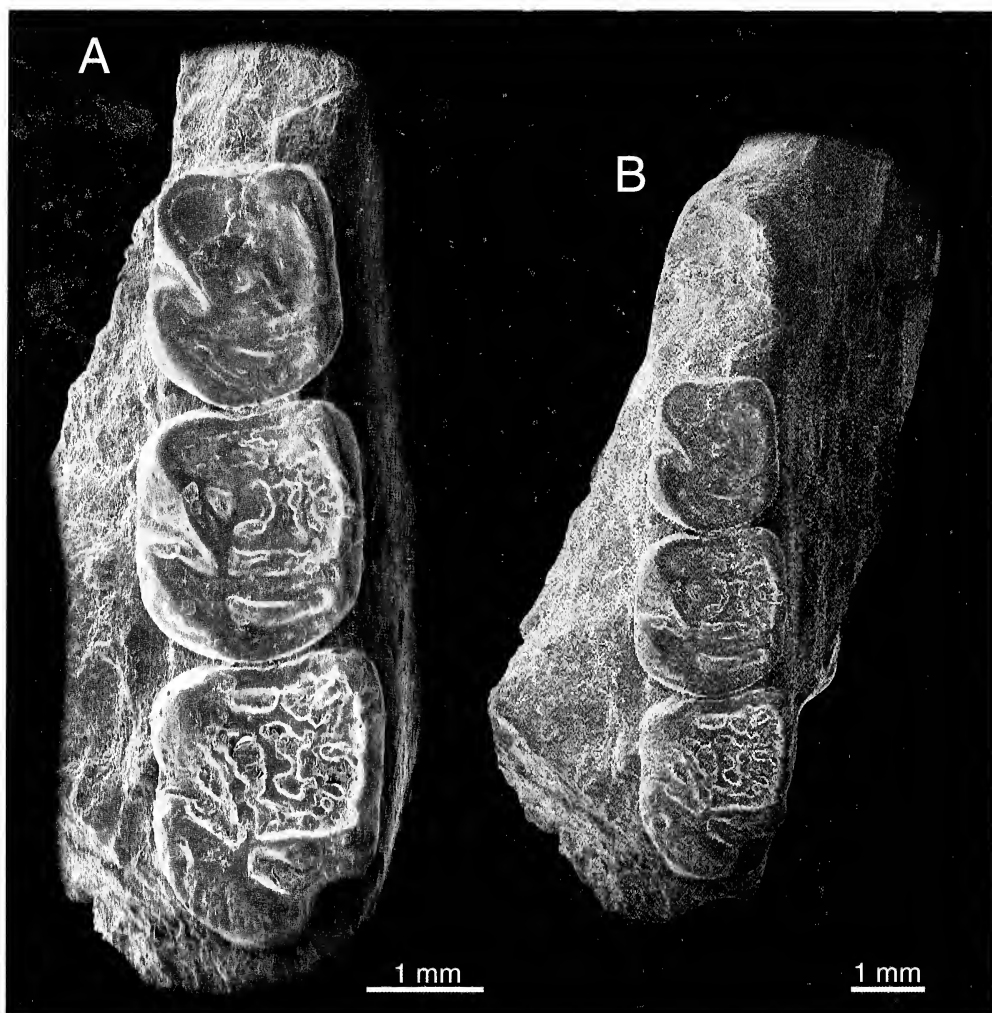


Fig. 2.—*Pondaunginys anomaluopsis*, new genus and species, holotype: NMMP-KU 0213, left mandibular fragment with M_{1-3} . A. Occlusal view of teeth. B. Entire specimen showing jaw structure.

Etymology.—For the genus, Pondaung Formation, and *mys*, Greek, mouse; for the species, Gr. *anomaluros*, different, and *opsis*, like, referring to the familial affinities of this rodent.

Description.—An incomplete left mandible with M_1 – M_3 and the alveolus of P_4 , NMMP-KU 0213 (Fig. 2), represents a new taxon of anomalurid rodent. The mandible appears to have been sturdily built. At the diastema the mandible drops down only gradually anterior to the alveolus of P_4 . There appears to have been a mental foramen high on the jaw below the diastema just anterior to the alveolus of P_4 . The masseteric fossa is deeply concave and extends forward to below the trigonid of M_2 ; its ventral ridge continues forward to below the middle of M_1 . The mandible differs from that of Recent *Anomalurus* but shares some characters with species of the Miocene *Paranomalurus* (Lavocat, 1973): the lack of a drop of the mandible anterior to P_4 occurs also in *P. soniae*, whereas the distinct masseteric fossa can be found in *P. bishopi*. Unfortunately, the posterior-most part of the mandible, including the coronoid and condyloid processes and the angle, is not preserved.

The alveolus suggests that P_4 was longer than M_1 . The molars, which increase in size from M_1 to M_3 , have occlusal surfaces with well-developed main crests and numerous lesser crenulations and also are surrounded lingually by an elevated cingulum of enamel. They are distinctly more lophate than cusate.

Table 1.—Measurements (in mm) of *Pondaung anomalurids* (all NMMP-KU numbers).

	<i>P. anomaluropsis</i>		<i>?P. anomaluropsis</i>		anomalurid sp. 1		anomalurid sp. 2			
	0213 (holotype)		0049		0047		0231		1533	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
M ₁	2.6	2.2	—	—	—	—	ca. 2.3	2.1	2.2	2.0
M ₂	2.7	2.5	2.8	2.5	2.8	2.8	2.3	2.2	—	—
M ₃	3.2	2.6	3.1	2.2	—	—	2.5	2.2	—	—

The first lower molar is worn heavily enough to have some of the pattern on the trigonid obliterated. Still prominent features of the occlusal surface are as follows: a strong anterolophid between protoconid and metaconid; an ectolophid extending obliquely posterolingually from protoconid to the intersection of hypoconid and hypolophid; a mesolophid that has complex subdivisions lingually; a hypoconid that is canted anterobuccally; a long, straight hypolophid; and a strong, posteriorly convex posterolophid that, with the hypolophid, encloses a transversely elongate valley.

The less worn M₂ preserves more detail of the pentalophodont occlusal surface. Antero- and posterolophid, ectolophid, and hypoconid-hypolophid resemble those on M₁. In addition, M₂ preserves the metalophulid I, which is complex lingually—appearing to bifurcate and have a short posteriorly extending process. The mesolophid appears to be double at the ectolophid junction, and its more posterior extension is bifurcate lingually.

The last lower molar, the largest of the three, is similarly complex. It differs from M₂ mainly in having a posterolophid that protrudes more posteriorly. The posterolingual part of the posterolophid is broken from the specimen, so its full extent is not determinable.

Probably also referable to *P. anomaluropsis* is NMMP-KU 0049, a left mandibular fragment with M₂₋₃ so badly eroded that very little pattern remains. Traces of multiple lophids suggest that this is an anomalurid, and its size (Table 1) puts it near *Pondaungimys*. It is from Wka or Kdw locality (Mogaung area, Fig. 1; Tsubamoto et al., 2000, fig. 7, pl. 1 I; the specimen was collected by local villagers, so the exact locality is not certain).

Anomalurid sp. 1

NMMP-KU 0047 (Fig. 3A), a left M₂, has a somewhat similar but more complex occlusal pattern than that of *Pondaungimys*, and the tooth is larger and relatively wider transversely than those of *Pondaungimys*. Because the sample size of Pondaung rodents is too small to provide any indication of individual variation, this specimen is tentatively considered to represent another anomalurid taxon. It is from Wka or Kdw locality (Mogaung area, Fig. 1; Tsubamoto et al., 2000, fig. 7, pl. 1 G).

Anomalurid sp. 2

NMMP-KU 1533 (Fig. 4A), a right mandibular fragment with M₁ and alveoli for the other cheek teeth (Pk1 locality, Bahin area), and NMMP-KU 0231 (Pk2 locality, Bahin area; Fig. 1; Tsubamoto et al., 2000, fig. 5, pl. 1 D–F), a right mandibular fragment with M₁–M₃ (Fig. 4B), represent a smaller species. Both specimens have more worn teeth than NMMP-KU 0213 of *Pondaungimys*. The remaining pattern and basic pentalophodont structure indicate that this is an anomalurid, probably close to *Pondaungimys* if not the same genus. The mandible of NMMP-KU 1533 has a deep masseteric fossa and strong ventral ridge as in *Pondaungimys*.

Anomalurid sp.

NMMP-KU 0048 (Fig. 3B), a right maxillary fragment with P³⁻⁴, has the size and morphology that suggest reference to *Pondaungimys anomaluropsis*. The anterior root of the zygoma occurs in line with P³ to the middle of P⁴, and juts out at a greater angle than in a similarly sized *Sciuravus*, suggesting that there may have been an enlarged infraorbital

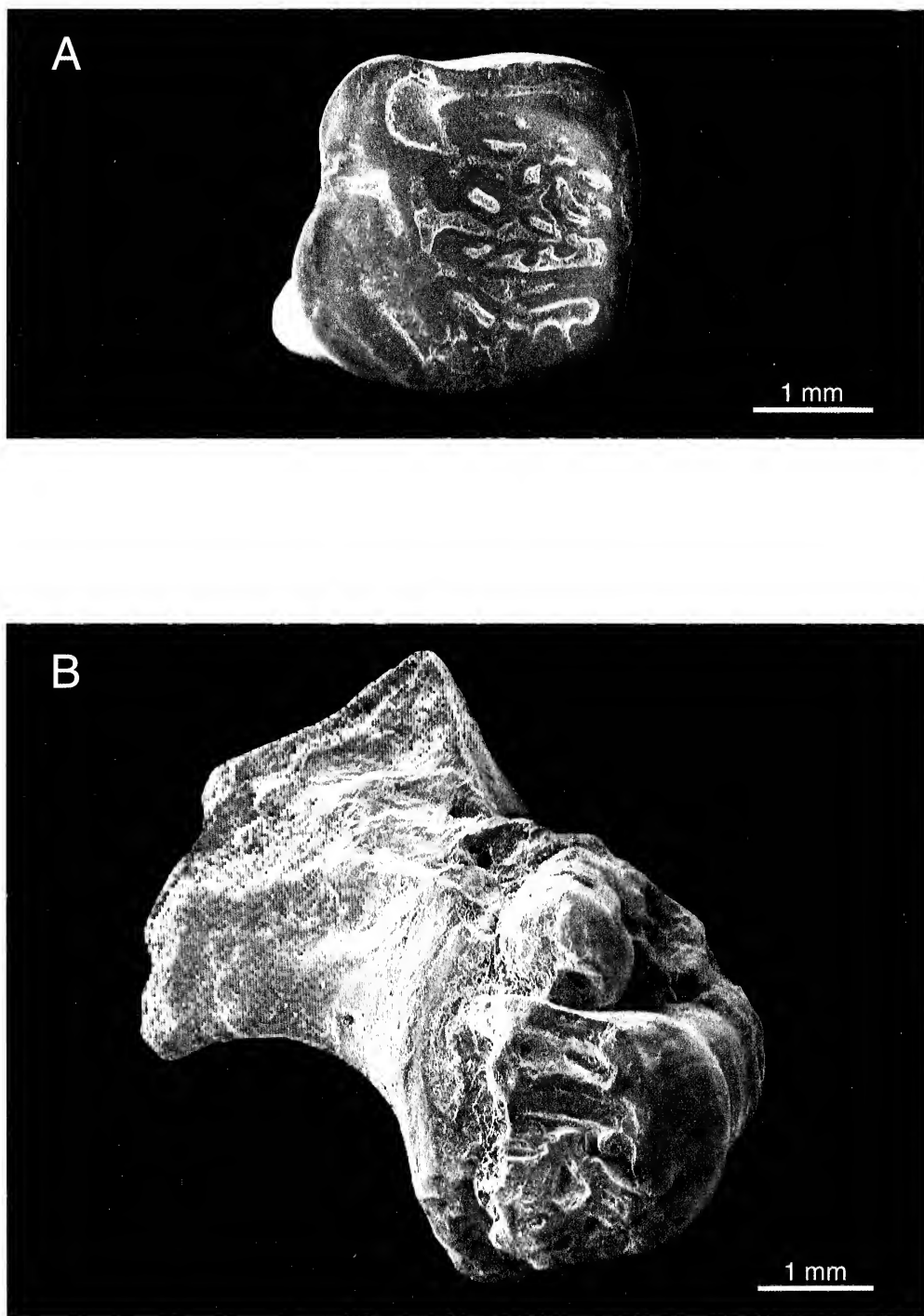


Fig. 3.—A. Anomalurid sp. 1, NMMP-KU 0047, occlusal view of left M₂. B. Anomalurid sp., NMMP-KU 0048, occlusal view of maxillary fragment with P₃₋₄.

foramen as in modern anomalurids. P^3 is a simple peg (anteroposterior, 0.9 mm; transverse, 1.1 mm). This tooth is absent in Miocene and later members of the family. P^4 , broken buccally, preserves a strong cingulum around the remaining sides (anteroposterior, 2.4 mm). It has a distinct protoloph, long mesoloph that bifurcates lingually, sending one arm to the metaloph, and a complete metaloph. The hypocone is set off by a small lingual notch, but as is the case with the lower molars, the tooth is basically more lophate than cusped. NMMP-KU 0048 is from Wka or Kdw locality (Mogaung area, Fig. 1; Tsubamoto et al., 2000, fig. 7, pl. 1H).

DISCUSSION

Although the family Anomaluridae has been listed as a component of several Paleogene faunas (Krabi, Thailand; Taqah, Oman; Bugti, Pakistan), the only previously described Eocene anomalurid is *Nementchamys lavocati* from the ?late Eocene Bir El Ater or Nementcha locality of the Nementcha Mountains of Eastern Algeria (Jaeger et al., 1985). A taxon based on isolated upper and lower teeth, *Nementchamys* has distinctly anomalurid features in its basically pentalophodont lower molars, complete lingual wall of the lower molars and buccal wall of the upper molars, and the somewhat concave occlusal surfaces of the cheek teeth. *Pondaungimys* and *Nementchamys* clearly share many dental characters, although the latter is more derived in complexity of accessory crests.

The origin of the Anomaluridae was traced to the late early or early middle Eocene Zegdoumyidae (Vianey-Liaud et al., 1994; Vianey-Liaud and Jaeger, 1996), which are known from Glib Zegdou (Algeria) and Chambi (Tunisia). Three genera have been recognized, *Zegdoumys*, *Glibia*, and *Glibemys*, based on twenty-nine isolated teeth. These genera, which exhibit a variety of dental morphologies, have different degrees of similarity to anomalurids. This is shown especially in early stages of pentalophodonty, multiplication of accessory crests, and some development of a lingual wall on the lower cheek teeth. Of them, *Glibia pentalopha* is most similar to *Pondaungimys* in development of transverse lophs, and *Glibemys algeriensis* is most similar in morphology of the lingual wall of the lower molars. However, *Pondaungimys* is more derived than any of the Zegdoumyidae in having the characteristic anomalurid features of a complete lingual wall of the lower cheek teeth and more distinct pentalophodonty. On the other hand, the zegdoumyids are more derived than *Pondaungimys* and other anomalurids in absence of a complete ectolophid in the lower molars (Vianey-Liaud et al., 1994), a character shared with the Gliridae (Hartenberger, 1971) as well as with some Sciuravidae (Korth, 1984).

Morphological and biogeographic considerations led Vianey-Liaud and Jaeger (1996) to hypothesize an ancestral position of the Zegdoumyidae to both the graphiurine Gliridae (elevated by them to family Graphiuridae) and the Anomaluridae. The first postulate, relationships between Zegdoumyidae and graphiurines, is supported by their dental morphology. However, the suggestion of affinities between the zegdoumyids and the anomalurids is less well supported by known fossils. The very strong ectolophid and complete lingual wall on the lower cheek teeth in both the oldest-known anomalurids, *Pondaungimys* and *Nementchamys*, for example, are marked differences from zegdoumyids, *Graphiurus*, and other glirids.

A more complete fossil record would help in determining relationship among these families, but for the Gliridae, including *Graphiurus*, and Anomaluridae, molecular evidence from living forms provides some additional evidence. For example, the Gliridae have been shown to group with the Sciuroidea, based on an analysis of the combined data from three genes, whereas the Anomaluridae group with a "mouse-related clade" that includes Castoridae, Geomyoidea, and Myodonta (Huchon et al., 2002). A study of the GHR gene shows, further, that *Graphiurus* groups as do the other glirids with the sciurid-aplodontid

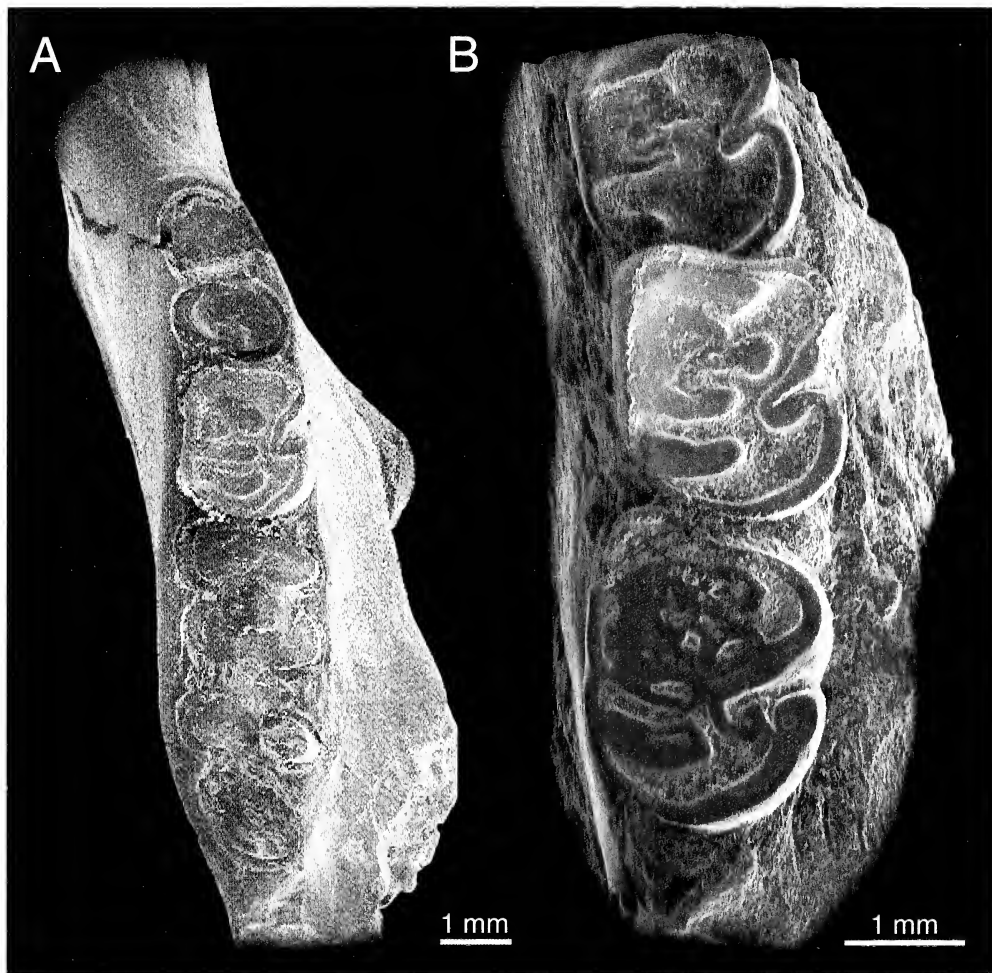


Fig. 4.—Anomalurid sp. 2. A. NMMP-KU 1533, occlusal view of right mandibular fragment with M_1 and alveoli for the other cheek teeth. B. NMMP-KU 0231, occlusal view of right mandibular fragment with M_1 – M_3 .

clade (Waddell and Shelley, in press). Although the source of the anomalurids is still not clear, molecular evidence does suggest a separate origin for anomalurids and glirids. The role of the zegdoumyids in this scheme is here interpreted to involve, on the basis of an admittedly incomplete fossil record, close relationships to glirids but not to anomalurids.

Biogeographic considerations show that glirids are known to have inhabited southern France by the end of the early Eocene, Paleogene Mammal Level MP 10 (Escarguel, 1999). Thus, the fossil record could support the concept of a migration by glirids from southern Europe into Africa and origin there of the zegdoumyids. No glirids are known from Asia until the latest Oligocene, precluding such a source for the zegdoumyids. As for the anomalurids, presence of *Pondaungimys* in southeast Asia opens the possibility of phylogenetic connections with several groups of non-ctenodactyloid Asian rodents, but whether with ischyromyids or others remains a matter of speculation.

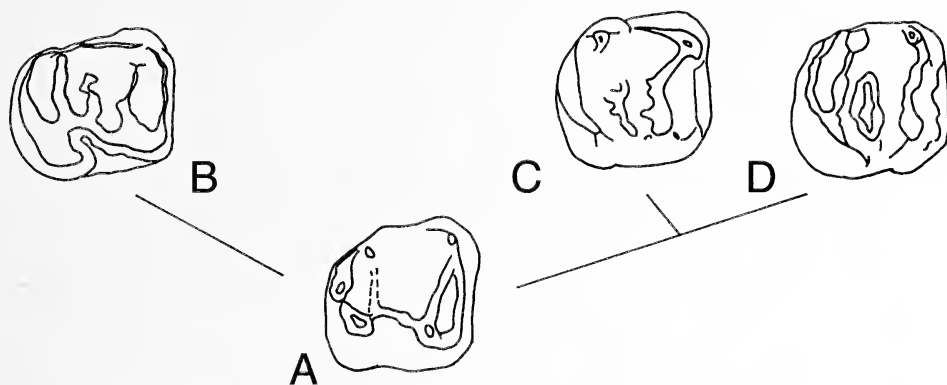


Fig. 5.—Occlusal surfaces of lower M_{1or2} of an ischyromiid, an anomalurid, a glirid, and a zegdomyid, comparing the primitive condition having a complete ectolophid (A, *Eoischyromys* from the middle Eocene of China, and B, *Pondaungimys*) with the derived reduction or absence of it (C, *Gliravus robiacensis* of MP 16 of France, and D, *Glibia pentalopha*). After: A, Wang et al., 1998; B, This paper; C, Hartenberger, 1971; and D, Vianey-Liaud et al., 1994.

Pondaungimys is the oldest anomalurid currently recognized, as well as the oldest indication of the family in Asia. Suggestion of some diversity within the family in the Pondaung localities may imply a still earlier record in southeast Asia, allowing time for diversification in the wet coastal area represented by the fluvio-deltaic depositional setting of the upper part of the Pondaung Formation (Aung et al., 2002). The occurrence of anomalurids in the Pondaung fauna and in the younger Krabi locality of Thailand and in the Nementcha locality of Algeria is another indication of faunal exchange between Africa and southeastern Asia in the middle to late Eocene, documented also among other rodents, Primates and Artiodactyla (Chaimanee et al., 1997; Ducrocq et al., 1997; Marivaux et al., 2000). The dispersal of these rodents probably occurred by the end of the middle Eocene, but neither the precise route nor the environmental conditions for the faunal exchange are known. Lack of any trace of anomalurids in the known fossil record of central Asia seems to indicate that the migration took place south of the Tethys Sea.

The Neogene record of anomalurids can be traced to *Paranomalurus* and *Zenkerella* from the early Miocene of Kenya. Dentally these genera are very similar to extant anomalurids, and an ulnar fragment suggests that the gliding locomotion used by *Anomalurus* and *Idiurus* had developed by that time (Lavocat, 1973).

Both *Pondaungimys* and *Nementchamys* have dental patterns that are more complex than in Miocene and later anomalurids, in which five or fewer transverse lophs provide the only pattern on the cheek teeth. Recent anomalurids feed on sap, bark, flowers, leaves, fruit, and insects (Julliot et al., 1998). The complexity of crests in the occlusal pattern of the cheek teeth in Eocene anomalurids suggests different feeding habits, but the functional significance of complex folds on rodent molariform teeth, present also in such Eocene rodents as *Thisbemys*, *Lophiparamys*, and *Eutypomys*, is not yet clear.

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Recent specimens of anomalurids for comparative work. Mark Klingler prepared the illustrations. Thanks are also due to Professor Nobuo Shigehara (Primate Research Institute, Kyoto University) for his financial support and encouragement for this work, and to Drs. Yukimitsu Tomida (National Science Museum, Japan) and Patricia A. Holroyd (University of California) for their help in collecting literature. This research was supported by the Overseas Scientific Research Funds (No. 14405019 to N. Shigehara) and the 21st Century COE Program of Kyoto University (Leader, T. Nishida) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

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JELLISONIA PAINTERI (SIPHONAPTERA: CERATOPHYLLIDAE),
A NEW SPECIES OF FLEA FROM GUATEMALA

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ABSTRACT

A new montane species of flea, *Jellisonia painteri* (Ceratophyllidae: Ceratophyllinae), is described from the cloud forests of the Sierra de las Minas (2200 m), Departamento de Zacapa, Guatemala. This is the first published record of *Jellisonia* in Guatemala. Specimens were collected from *Habromys lophurus* (Osgood, 1904), *Peromyscus grandis* Goodwin, 1932 and *Reithrodontomys microdon* Merriam, 1901. The preferred host of this new species appears to be *H. lophurus*. *Jellisonia ironsi* (Eads, 1947) and *Jellisonia wisemani* Eads, 1951 are also reported for the first time from Guatemala.

KEY WORDS: *Jellisonia painteri*, flea, Siphonaptera, Guatemala

INTRODUCTION

The montane regions of Guatemala are poorly known biologically and the fleas from that region are no exception. A network of scientists from Central America and the United States initiated an expedition in 1998 to study cloud forest mammals and their parasites in the Sierra de las Minas, Guatemala. Among this material was a new species of flea belonging to the genus *Jellisonia* Traub, 1944. This is the first report of the genus *Jellisonia* in Guatemala. In general, the genus *Jellisonia* occurs from north central Texas, U.S.A. to southern Panama, although few records have been published from south of Chiapas, Mexico. Smit (1958) reported one female of *Jellisonia ironsi* (Eads, 1947) from "road from San Salvador to Santa Ana, at km 35", El Salvador from *Baiomys musculus griseus* = *Baiomys musculus* (Merriam, 1892); Tipton and Mendez (1961) described *Jellisonia johnsonae* from Cerro Punta, Panama on *Scotinomys teguina episcopi* = *Scotinomys teguina* (Alston, 1877), and Tipton and Mendez (1966) reported additional specimens of *J. johnsonae* from near the type locality. The latter authors also reported a female specimen as a probable undescribed species in Los Santos Province, Panama. The senior author is currently revising the genus *Jellisonia* and has examined most of the known specimens represented in this genus. Among material from the Robert Traub collection (Carnegie Museum of Natural History, Pittsburgh, PA) additional unreported records of *J. ironsi* occurring in Costa Rica have been examined. A detailed description of these specimens will be given elsewhere.

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The purpose of this paper is to describe a new species of *Jellisonia* from Guatemala and to report additional species of the genus that occur in Guatemala that have not been reported previously.

MATERIALS AND METHODS

A study site was established in the cloud forest (2,200 m elevation) located along the Rio Hondo, in the Reserva de Biosfera, 6 km NNW of San Lorenzo (15°08'26"N, 89°40'36"W), Departamento de Zacapa, Sierra de las Minas, Guatemala. Three trap lines were set each night from 8–17 April 1998 using Sherman live traps, museum specials, and rat traps to capture small mammals. Traps were baited with a mixture of peanut butter, rolled oats, bacon and raisins. Mammals were individually placed in separate plastic bags at the capture site, euthanized, and brought to the processing area. Animals were brushed with a stiff bristle brush over a white enamel pan to obtain fleas. Fleas were preserved in 70 per cent ethanol and later treated with 10 per cent potassium hydroxide, dehydrated in a series of ethanol washes, further cleared in xylene, and mounted on slides in Canada balsam. A second site was established at La Cabana (15°04'54"N, 89°55'59"W), Departamento de El Progreso in the Reserva de Biosfera, and the same trapping and flea collection techniques were employed from 2–12 May 1998 as were reported April 8–17. Several specimens are also included that were collected in July 1996 from the San Lorenzo site.

Anatomical terminology used herein follows that of Rothschild and Traub (1971); however, reference is made to two "inverse setae" on the anterior apical margin of the distal lobe of st.(sternite) IX that are not described in their glossary of terminology (Fig. 1D). These are herein defined for future reference. These two setae are close together, one dorsal and the other ventral. The ventral seta is always the larger of the two. The small dorsal seta is present in all species of *Jellisonia*, although it has been omitted in the literature in most illustrations of the ninth sternum. A few species of *Kohlsia* possess this character, but it is otherwise restricted to the genus *Jellisonia*.

An Olympus BX61Compound Microscope, Olympus CV12 digital camera, Olympus Microsuite™ B3SV program, and Adobe Photo Shop 7.0 were used to prepare digitized images.

The overall body dimensions of males and females were measured from the foremost portion of the frons to the posterior margin of the telomere in males and to the posterior border of the sensillar plate in females.

RESULTS AND DISCUSSION

Jellisonia painteri Hastriter and Eckerlin, new species

Type Material.—GUATEMALA. **Zacapa Department**: Rio Hondo, Sierra de las Minas, 6 km NNW San Lorenzo (15°08'26"N, 89°40'36"W), 2200 m, ex *Habromys lophurus* (Osgood, 1904) [Host animal voucher specimen (MANCA-524) in collection of Universidad de San Carlos de Guatemala and host tissue voucher specimen (SP 13349) in Carnegie Museum of Natural History, Pittsburgh, PA], 12 April 1998, R. P. Eckerlin, male holotype and 4♀ paratypes; following types with same data as holotype except 13–17 April 1998, 5♂, 7♀ paratypes; Rio Hondo, Sierra de las Minas, 6 km NNW San Lorenzo (15°08'26"N, 89°40'36"W), 2200 m, ex *Peromyscus grandis* Goodwin, 1932, 10 April 1998, R. P. Eckerlin, allotype; following types with same data as allotype except 9–13 April 1998, 5♂ paratypes; following types with same data as allotype except ex *H. lophurus*, 1 and 4 July 1996, S.G. Perez, 1♂, 1♀ paratypes; and following with same data as allotype except ex *Reithrodontomys microdon* Mirriam, 1901, 4 July 1996, S. G. Perez, 1♂, 1♀ paratypes. Holotype (USNM Type No.105757), allotype and 6 paratypes (3♂, 3♀) deposited in the National Museum of Natural History, Washington, D.C.; 6 paratypes (3♂, 3♀) in the Carnegie Museum of Natural History, 4 paratypes (2♂, 2♀) in the Michael W. Hastriter collection, and the remaining paratypes (4♂, 5♀) in the Ralph P. Eckerlin collection.

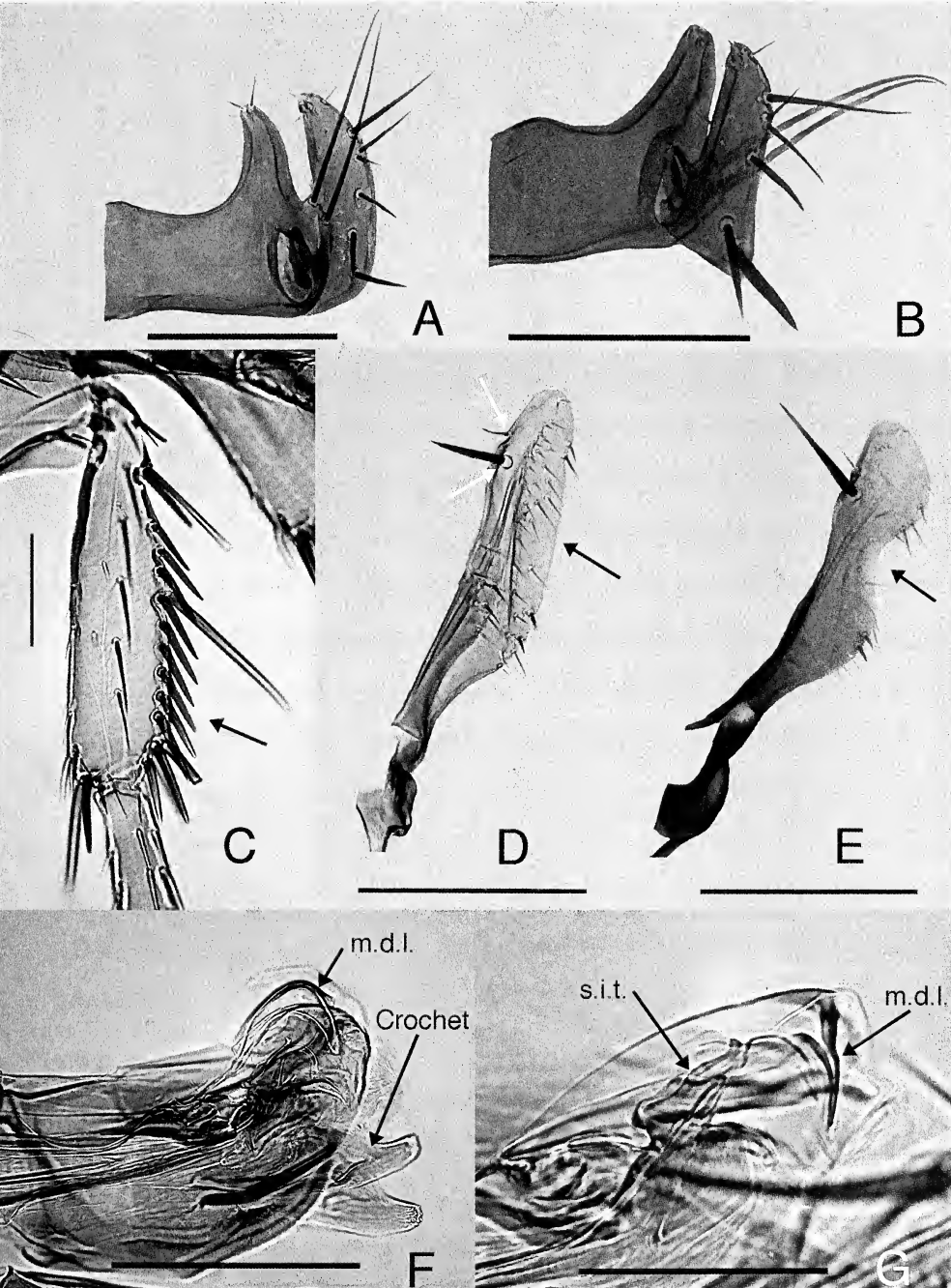


Fig. 1.—A. *Jellisonia painteri* n. sp. Basimere and telomere (paratype). B. *J. guerrensis*. Basimere and telomere. C–D. *J. painteri* (paratype). C. Hind tibia of female (arrow to comb). D. Distal arm of ninth sternum (black arrow: entire margin; white arrows: ventral and dorsal inverse setae). E. *J. klotsi*, ninth sternum (arrow depicts sinus). F. *J. painteri*, apex of aedeagus (m.d.l. = median dorsal lobe) (paratype). G. *J. guerrensis*, apex of aedeagus (s.i.t. = sclerotized inner tube). Scale = 100µ.

Diagnosis.—Among those species of *Jellisonia* that have distinctive combs along the dorsal margin of the mid and hind tibiae (Fig. 1C), *J. painteri* is most closely related to *J. klotsi* Traub, 1944 and *J. guerrenderensis* Morales, 1990. The new species is distinguished in the male by the smoothly rounded apex of the median dorsal lobe (m.d.l.) (Fig. 1F) and the slightly convex caudal margin of the distal arm of st. IX (Fig. 1D). In *J. klotsi* and *J. guerrenderensis*, the apex of the m.d.l. is acutely pointed (Fig. 1G) and the caudal margin of st. IX has two lobes separated by a shallow sinus (Fig. 1E). They also differ in details of the crochet, shape of the telomere, and other features of the aedeagus. Females may be separated from all other species that have combs on the meso- and metatibiae, except *J. klotsi*, *J. guerrenderensis*, and *J. hayesi hayesi*, by the presence of a large dorsal lobe subtended by a distinct sinus on the caudal margin of st. VII (Fig. 2D). The number of setae occurring on each side of st. IV–VI varies in the new species with two or three. Some specimens possess two setae per side on st. IV–VI, while others bear three per side. Those with two must be separated from *J. klotsi* and *J. guerrenderensis*, which consistently possess two per side. In these cases, they may be separated by locality since *J. klotsi* and *J. guerrenderensis* are not known to occur in Guatemala. For those specimens with three setae per side on st. IV–VI, they are similar to *J. h. hayesi* but differ by the sclerotized portion of the bursa copulatrix. The perula is reflected rearwards in *J. painteri* (Fig. 2D), while this structure is straight in *J. h. hayesi*. In addition, *J. h. hayesi* is not known to occur in Guatemala.

Description.—Head (Fig. 2A–B): Frons evenly rounded with slight indication of frontal tubercle in both male and female. Ventral ocelli close to oral angle. Preantennal setae composed of three major rows, anterior row of 6 setae separating punctate anterior area of frons from smooth lateral surface of ocular area; second row of 4 setae, and ocular row of 3 setae. Single small seta at oral angle. Postantennal region with three rows of setae (3, 6, and 6 in male; 3, 5, and 7 in female); posterior row of each with intercalary setae. Antennal falx dividing head in male but not reaching dorsum in female. Sparse row of minute setae along dorsal margin of antennal fossa; female with heavily sclerotized rim along dorsal margin, several setae anterior to rim. Indication of shallow occipital sulcus in male. Setae along apex of scape and pedicel at most reaching next segment. Male antennae extending onto prosternum, female antenna much shorter. Eye pigmented and entire. Trabecula centralis present. Four segments of maxillary palpus each subequal in length. Maxilla tapering to narrowly extended point. Labial palpus of 5 segments, apical segment nearly twice length of other segments; apex not extending to apex of procoxa.

Thorax (Fig. 2C): Pronotum with single row of setae with intercalaries. Pronotal comb of 18–20 spines ($n=8$) in male and 20–22 ($n=8$) in female. Mesonotum and metanotum each with 2 rows of setae, metanotum with scattered setae anterior to rows. Intercalary setae present in main rows of each. Mesonotum with 3–4 pseudosetae under collar. Nine setae on metapleuron (mesipsternum and mesepimeron). Lateral metanotal area with 2 setae; pleural arch well developed. Metepisternum with single large seta; squamulum present. Metepimeron with three vertical rows of setae, usually 3, 3, 1 but number variable; all setae below level of spiracle.

Legs (Fig. 1C): Procoxa broad, width nearly half the length of segment, with many lateral setae. Mesocoxa with sparse setae along ventral half of anterior margin; setae extended along entire anterior margin of metacoxa. Lateral oblique break line of mesocoxa extending across half of coxa. Profemur with 7–8 lateral setae and a single seta on mesal surface. Tibiae of each leg with single lateral vertical row of setae and large supernumerary setae along dorsal margin forming a comb, particularly below the fifth dorsal notch of meso- and metatibiae. Metatibia with single vertical row of minute setae on mesal surface. Protarsus I with comb of 3 setae on posterior margin. Distitarsomere of each leg with 5 lateral plantar bristles, the first pair shifted onto plantar surface. Two stout preapical plantar bristles on protarsus V, each hair-like on meso and metatarsus V.

Unmodified Abdominal Segments: Two rows of setae on each tergite; anterior row with diminishing numbers of setae from anterior to posterior. Main row with intercalary setae. One seta below level of spiracles. Usually t. (tergite) I–III with marginal spinelets (1, 2, 1 per side), respectively. Occasional specimen with spinelet on t. IV. Anterior ventral margin of t. II with distinct sclerotization, greater in female than male. Male and female each with 3 antesensilial bristles. Those of male borne on projection, middle bristle large, dorsal and ventral bristles very small. Middle bristle of female longest, dorsal and ventral bristles about 1/3 and 4/5 length of middle bristle, respectively. Spiracles round posteriorly. Sternites II–VII of male each with 2 setae per side; number in female variable with 2 or 3 setae per side on st. II–VI.

Modified Abdominal Segments, male (Fig. 1A, 1D): Tergum VIII large, expanded over t. IX; adorned with group of 5–6 dorsal setae and 1–2 ventral setae. Spiracle VIII notably displaced caudally at posterior margin of sensilial plate. Process 1 of t. IX finger-like with 3 small apical setae; below 3 setae is a small circular clearing

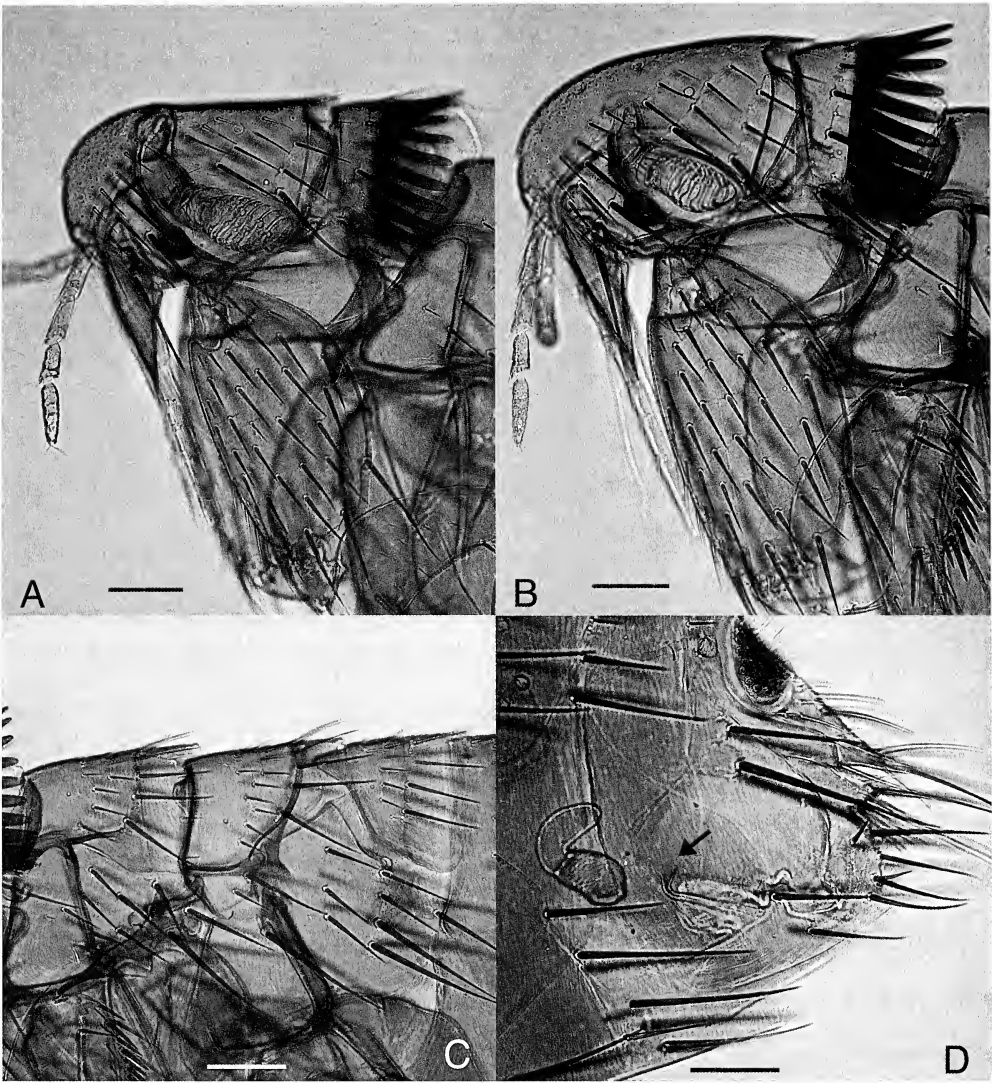


Fig. 2.—A–D. *Jellisonia painteri* n. sp. A. Head and pronotum, male (paratype). B. Head and pronotum, female (allotype). C. Thorax, female (allotype). D. Female terminalia, seventh sternum, spermatheca, and bursa copulatrix (arrow: reflexed bursa copulatrix). Scale = 100 μ .

(7–8 μ) resembling the fovea on the basimere of *Megarhroglossus* Jordan and Rothschild, 1915. Two acetabular bristles borne on slight projection separated by a space three times their basal width. Telomere with parallel sides, bluntly rounded at apex, with 5 stout setae along caudal margin; 2 dorsal setae smaller and directed caudad, 3 ventral setae spiniform, placed on mesal surface and directed ventrad with long axis of telomere. Lateral patch of 8–10 minute setae on proximal half of telomere. Sternum VIII reduced, pencil-like with apical long bifurcate membranous lobes. Convoluted membrane between st. VIII and st. IX with medial pair of spiculated bulbous structures. Sternum IX fused at base, with membranous point of flexure approximately 1/5th from base of distal arm. Distal arm setiferous along posterior half, with two small spiniform setae near ventral caudal margin. Ventral inverse seta long, slender, set back from margin; dorsal inverse seta marginal and much smaller. Mesal groove traversing length of distal arm. Tendon of st. IX extending well beyond aedeagal apodeme. Apex of proximal arm of st. IX fused with manubrium of t. IX and proximal spur of aedeagus.

Aedeagus (Fig. 1F): Sides of aedeagal apodeme nearly parallel. Proximal spur present. Accessory lateral lobes present. Membranous disto-lateral lobe extends beyond median dorsal lobe. Apical sclerite of median dorsal lobe thickened and rounded at apex. Lateral lobe semi-sclerotized, extending upward and over disto-lateral lobe and median dorsal lobe. Crescent sclerite short, satellite sclerite present. Sclerotized inner tube broad proximally, tapering to apex; with short arching fistula. Dorsal armature very long (twice length of sclerotized inner tube). Crochet with heavily sclerotized basal margin; paxillus present, tuberculate at apex. Penis rods extend well beyond apex of aedeagal apodeme, without coil.

Modified Abdominal Segments, female (Fig. 2D): Patch of 4–6 small setae on t. IX postad to antesensilial bristles. Tergum IX large with dorsal group of 2–4 setae, ventral group of 1–2 setae, apical marginal group of 3–4 setae, and 2 short subspiniform setae in an oblique row from margin toward sensillum. Large dorsal and ventral lobes on caudal margin of st. VII forming a deep sinus; lateral row of 4–5 setae. Anal stylet four times as long as wide; long apical seta, shorter ventral seta, and minute dorsal seta close to apex. Ventral anal lobe angulate on ventrocaudal margin; bearing 4 long stout setae, dorsal most seta separated from ventral three setae by space wider than width of base of setae. Sternum VIII broad, with small lobe at apex; coarse rugulose pattern running with long axis of sclerite. Bursa copulatrix subequal in length to spermatheca; perula reflected caudad. Hilla and bulga of spermatheca subequal in length.

Dimensions (slide mounted specimens).—Average length of males, 2.3 mm, range: 2.2–2.4 mm ($n = 12$); Average length of females, 2.7 mm, range: 2.4–3.1 mm ($n = 15$).

Etymology.—This species is named in honor of the late Harry F. Painter, distinguished citizen, American veteran war hero, entomologist, and friend.

Remarks.—A comparison of the hosts collected at the San Lorenzo and La Cabana sites is noteworthy. While the number and composition of the small mammals collected at each site were similar, neither the new species nor other species of *Jellisonia* were collected from hosts at the La Cabana site. The San Lorenzo site yielded a total of 118 small mammals [*P. grandis* ($n = 96$) and *H. lophurus* ($n = 22$)] and the La Cabana site 128 mammals [*P. grandis* ($n = 115$) and *H. lophurus* ($n = 13$)]. Six of 96 *P. grandis* (6.3 %) and 11 of 22 *H. lophurus* (50%) were infested with one or more *J. painteri* at the San Lorenzo site. The average number of fleas (flea index) per positive infested *P. grandis* and *H. lophurus* was 1.0 and 1.54, respectively. Why specimens of *Jellisonia* were not obtained from the same host animals examined at the La Cabana site is not known. Weather was similar, trapping/collecting techniques were conducted in the same manner, and the work was carried out less than four weeks after the San Lorenzo collections.

Jellisonia wisemani Eads, 1951

Material Examined.—GUATEMALA. Chiquimula Department: 2.4 km NW Esquipulas, 945 m, (14°34'N, 89°21'W), ex *Peromyscus* sp., 6 March 1952, L. de la Torre, 1♀, 12 March 1952, 2♂, 1♀; 4 km ENE and 4.8 km SE Esquipulas, ex *Oryzomys* sp., 13 March 1952, L. de la Torre, 1♂; and 4 km ENE Esquipulas, 915 m, 12 March 1952, L. de la Torre, 2♂, 1♀ [Robert Traub collection, Carnegie Museum of Natural History (CMNH)].

Remarks.—*Jellisonia wisemani* is reported for the first time in Guatemala and represents an extreme southern record for this species. The nearest and unreported specimens examined (included in revision) is 325 km to the west in Chiapas, Mexico near the border of Mexico and Guatemala.

Jellisonia ironsi (Eads, 1947)

Material Examined.—GUATEMALA. Jutiapa Department: 1.6 km SE Jutiapa, 900 m (14°17'N, 89°54'W), ex *Baiomys* sp., 25 March 1952, L. de la Torre, 1♀ (CMNH).

Remarks.—This is a new record in Guatemala and the most southerly record for the species. Other specimens of *J. ironsi* hereunto reported in the literature were examined from Costa Rica but will be discussed in the revision of the genus *Jellisonia*. This species is relatively specific to both species of *Baiomys* and, insofar as now known, follows the distribution of these hosts rather closely.

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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. XIII.
ANNOTATED GAZETTEER OF MAMMAL COLLECTING SITES IN SURINAME

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ABSTRACT

The following data are presented for 70 sites in Suriname where scientific specimens of mammals were collected under the aegis of the Alcoa Foundation-Suriname Expeditions: specific localities, including latitude and longitude readings; dates when collections were made at the site; collectors/preparators working at the site; site description; and list of genera of mammals captured. The names and boundaries of many of the districts of Suriname, which are the major political subdivisions of the country, have changed since field work was completed in 1981. The sites are referenced to the new districts of the country.

KEY WORDS: gazetteer, Suriname, mammals, habitats, collecting sites

INTRODUCTION

Between 1977 and 1981, the Alcoa Foundation-Suriname Expeditions collected mammals in the northeastern South American country of Suriname. The specimens were deposited in the Section of Mammals of the Carnegie Museum of Natural History. With renewed work on mammals in this collection, it has become evident that there have been some major changes in the political geography of the country since our field research there. The district-level political subdivisions, which are the first major subdivisions of the country, have been completely reorganized and, in several cases, given new names. This means that the district names appearing on the tags of many of the mammal specimens from Suriname in the Carnegie Museum of Natural History have changed. This also is true of the district names published in previous reports from the Alcoa Foundation-Suriname Expeditions (Baker et al., 1981; Genoways and Baker, 1996; Genoways and Williams, 1980, 1984, 1986; Genoways et al., 1981; Honeycutt et al., 1981; Lim et al., 2003; Phillips, et al., 1984; Williams and Genoways, 1980a, 1980b; Williams et al., 1981). Previously, the districts in Suriname were oriented generally from north to south so that they encompassed some areas along the more densely populated coast and some of the lightly inhabited or uninhabited interior of the nation. With the reorganization, most of the districts are clustered near the coast, whereas the lightly developed interior is a single district—Sipaliwini. Because much of our work was conducted in the interior of Suriname, many of our localities will now fall in this district.

We also have taken this opportunity to add latitude and longitude readings to localities where none were recorded early in the research project and to review those calculated in the field. In the days before Global Positioning System units were used to precisely locate work sites, we relied on the available maps. The maps of Suriname during our work there were

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prepared by the Dutch and were done on a large scale (1:1,000,000). With new, higher resolution maps and up-to-date and online gazetteers, such as those of U. S. Government's National Imagery and Mapping Agency (www.nima.mil) and Global Gazetteer from Falling Rain Genomics, Inc. (www.calle.com/world/index.html), our collecting sites can be far more precisely located. In several cases, we have corrected the latitude and longitude readings for collecting sites. These are noted in the text below. These numbers have been changed in the database in the Section of Mammals, but the old latitude and longitude readings still appear on the original specimen tags with corrections shown in pencil.

The following people were involved in the field project as collectors and/or preparators, and their names appear on the original specimen field tags—Michael L. Arnold; Robert J. Baker; W. V. Branan; Murray H. de la Fuente; Hugh H. Genoways; Jane A. Groen; M. M. Held; Rodney L. Honeycutt; T. J. Jacobus; Ben J. Koop; Carlo Merton; K. Mohadin; Carleton J. Phillips; Henry Reichert; Leo Roberts; Paisley Seyfarth [= Cato]; J. J. Toto; Stephen L. Williams. The field notes from Suriname for these individuals also have the same issues as the specimen tags and database, and the field notes have not been altered from how they were originally written. Original district designations persist in the database, in agreement with the skin tags; however, the new district names are provided in the "Comments" field of affected specimen records.

In the annotated gazetteer below, the district names appearing as headings in all capital letters are the currently correct district names. In the specific localities, the district names used during our field work and recorded in the original records are in brackets. We have annotated the gazetteer with the dates when collections were made at the site and the names of the collectors/preparators working there with the hope that these data will make using the specimens and their associated data easier in the future. We also have included a brief description of each site and have given a list of genera that were taken so that other researchers can assess the area surveyed and the biodiversity of mammals that was documented.

ANNOTATED GAZETTEER

BROKOPONDO

[Brokopondo] Brownsberg Nature Park, 3 km S, 20 km W Afobakka, 04°59'N, 55°10'W

Collection date.—7 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—In the Browns Berg highlands just west of the lake Prof. Van Blommestein Meer. The area was covered in original tropical rainforest with a moderate understory, although open areas under the forest were not uncommon.

Genera present.—*Anoura*, *Artibeus*, *Didelphis*, *Eptesicus*, *Micronycteris*, *Monodelphis*, *Oryzomys*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Saccopteryx*, *Sturnira*, *Tonatia*

[Brokopondo] Brownsberg Nature Park, 5 km S, 21.5 km W Afobakka, 04°57.5'N, 55°12'W

Collection dates.—10–11 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—In the Browns Berg highlands just west of the lake Prof. Van Blommestein Meer. Trapping was done in thick second growth forest.

Genera present.—*Didelphis*, *Neacomys*, *Oryzomys*

[Brokopondo] Brownsberg Nature Park, 6 km S, 20 km W Afobakka, 04°57'N, 55°10'W

Collection date.—9 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—In the Browns Berg highlands just west of the lake Prof. Van Blommestein Meer. Bats were captured in a mist net placed at the entrance of an abandoned gold mine. The tunnel was approximately 12 meters deep, 2.5 m high, and 2 m wide. The vegetation in the surrounding area was dense tropical forest.

Genera present.—*Carollia*, *Glossophaga*

[Brokopondo] Brownsberg Nature Park, 7 km S, 18.5 km W Afobakka, 04°56'N, 55°09'W

Collection dates.—8–10 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—In the Browns Berg highlands just to the west of the lake Prof. Van Blommestein Meer. Traps and mist nets were placed along the trails and around the buildings of the park headquarters. The forest in the area was a mix of secondary and mature primary tropical forest.

Genera present.—*Anoura*, *Artibeus*, *Carollia*, *Didelphis*, *Neacomys*, *Oecomys*, *Oryzomys*, *Platyrrhinus*, *Proechimys*, *Rhinophylla*, *Sturnira*, *Tonatia*

[Brokopondo] Brownsberg Nature Park, 8.8 km S, 19.3 km W Afobakka, 04°55.5'N, 55°10'W

Collection date.—11 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—In the Browns Berg highlands just west of the lake Prof. Van Blommestein Meer. Traps were placed in dense secondary vegetation.

Genus present.—*Proechimys*

[Brokopondo] Brownsberg Nature Park, 10 km S, 23 km W Afobakka, 04°54'N, 55°11'W

Collection date.—9 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—In the Browns Berg highlands just west of the lake Prof. Van Blommestein Meer. The area was mature tropical forest with only a limited understory, but fallen trees were common.

Genera present.—*Didelphis*, *Myoprocta*, *Oryzomys*

[Brokopondo] Brownsberg Nature Park, 8 km S, 2 km W Brownsweg, 04°55'N, 55°10'W

Collection dates.—19–24 September 1979

Collectors/Preparators.—Genoways, Groen, Honeycutt, Phillips, Roberts, Williams

Site description.—In the Browns Berg highlands just west of the lake Prof. Van Blommestein Meer. Work was conducted around the park headquarters and adjacent roads and trails. The habitats sampled ranged from dense shrubbery along a road to second growth tropical forest to newly mature tropical forest to old mature tropical forest.

Genera present.—*Artibeus*, *Carollia*, *Eptesicus*, *Glossophaga*, *Lonchophylla*, *Micronycteris*, *Neacomys*, *Oryzomys*, *Philander*, *Phylloderma*, *Phyllostomus*, *Platyrrhinus*,

Proechimys, *Pteronotus*, *Rhinophylla*, *Saccopteryx*, *Sturnira*, *Tonatia*, *Trachops*, *Uroderma*

COMMEWIJNE

[Commewijne] Matapica, 06°00'N, 54°51'W

Collection dates.—15–16 September 1979

Collectors/Preparators.—Groen, Honeycutt, Roberts, Williams

Site description.—Collecting was done in dense coastal vegetation containing short shrubs and dense ground cover with some open mud flat areas.

Genera present.—*Oligoryzomys*, *Zygodontomys*

[Commewijne] Nieuwe Grond Plantation, 05°53'N, 54°54'W

Collection dates.—12–14 September 1979

Collectors/Preparators.—Groen, Honeycutt, Roberts, Williams

Site description.—Collecting was done around the plantation house and the nearby orchards and gardens, which included citrus and banana trees. There were mowed lawns in the vicinity of the plantation buildings and large stands of bamboo near the orchards. Beyond these areas were relatively short, secondary growth trees and shrubs.

Genera present.—*Artibeus*, *Carollia*, *Didelphis*, *Eptesicus*, *Glossophaga*, *Mesophylla*, *Micronycteris*, *Mimon*, *Philander*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Saccopteryx*, *Sturnira*, *Tonatia*, *Zygodontomys*

CORONIE

[Coronie] 4 km E Totness, 05°52'N, 56°16'W

Collection date.—28 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Bats were captured in an abandoned house.

Genera present.—*Carollia*, *Glossophaga*

[Coronie] Totness, 05°52'N, 56°19'W

Collection dates.—27–29 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps and mist nets were placed in a coconut plantation, with dense undergrowth. A few mango trees also were in the area.

Genera present.—*Artibeus*, *Caluromys*, *Carollia*, *Didelphis*, *Philander*, *Phylloderma*, *Platyrrhinus*, *Proechimys*, *Zygodontomys*

MAROWIJNE

[Marowijne] 4 km N, 10 km W Albina, 05°32'N, 54°08'W

Collection date.—2 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Trapping was conducted along the edge of, and into, a forested area. It was a difficult area in which to work because of many people and gardens along the road, heavy growth of vines at the edge of the forest, and swamps in other areas.

Genera present.—*Oryzomys*, *Proechimys*, *Zygodontomys*

[Marowijne] approximately 10 [20?] km NW Albina, 05°33'N, 54°09'W

Collection date.—26 September 1981

Collectors/Preparators.—Branan, Williams

Site description.—A single specimen of *Eira*, which was a gift from W. V. Branan, was taken at this place. The precise locality for this specimen is not known because of disagreement in its associated data. The specimen tag and museum catalog list the locality as “approximately 10 km NW Albina,” but the field preparator’s catalog lists the location as “approximately 20 km NW Albina.” There are no data available to resolve this conflict with any degree of certainty.

Genus present.—*Eira*

[Marowijne] 3 km SW Albina, 05°28'N, 54°05'W

Collection dates.—18, 20–24 October 1981

Collectors/Preparators.—Arnold, Groen, Jacobus, Koop, Roberts, Toto, Williams

Site description.—This location is along the Marowijne River, which forms the border with Guyane française. Vegetation in the general area was secondary rainforest. There was evidence of human disturbance in the area, including roads, trails, burning, and felled trees. Work was conducted in and along the forest, over small ponds in the area, along the trails and roads, and in areas with thorny bushes, shrubs, and grass.

Genera present.—*Artibeus*, *Carollia*, *Desmodus*, *Eptesicus*, *Glossophaga*, *Lonchophylla*, *Mesophylla*, *Micronycteris*, *Molossus*, *Monodelphis*, *Myotis*, *Neacomys*, *Oecomys*, *Oligoryzomys*, *Oryzomys*, *Philander*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Rhinophylla*, *Rhynchonycteris*, *Saccopteryx*, *Sphiggurus*, *Sturnira*, *Thyroptera*, *Tonatia*, *Uroderma*, *Vampyressa*, *Zygodontomys*

[Marowijne] 10 km N, 24 km W Moengo, 05°43'N, 54°38'W

Collection dates.—4–6 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Work was done on a Forest Service facility along the Perica River. The dominant vegetation in the area was tropical lowland forest, but there was a mix of other habitats, such as grassy and vine-covered openings in the forest, a marshy area, garden plots, and forest edge. Mist nets were placed in the forest, along the river, and around the building in which the team was staying because there were bats in the attic and roof. At one place, a series of mist nets was started in an open grassy area, ran along a trail through a forested area, and into another grassy opening.

Genera present.—*Artibeus*, *Carollia*, *Chiroderma*, *Desmodus*, *Glossophaga*, *Lonchophylla*, *Micronycteris*, *Molossus*, *Monodelphis*, *Myotis*, *Noctilio*, *Oryzomys*, *Philander*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Promops*, *Rhinophylla*, *Sturnira*, *Tonatia*, *Uroderma*, *Zygodontomys*

[Marowijne] Moengo, 05°37'N, 54°24'W

Collection dates.—2, 4 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Mist nets were placed in the vicinity of a hotel building in town where bats were seen to be emerging at dusk.

Genera present.—*Artibeus*, *Molossus*

[Marowijne] 1 km S Moengo, 05°36'N, 54°24'W

Collection date.—2 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Mist nets were placed over and near a pond that had developed in an old bauxite pit in an area surrounded by forest.

Genera present.—*Artibeus*, *Carollia*, *Molossus*, *Platyrrhinus*, *Sturnira*

[Marowijne] 2 km S Moengo, 05°36'N, 54°24'W

Collection date.—4 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps were set around the Moengo city dump.

Genus present.—*Zygodontomys*

[Marowijne] 20 km S Moengo, 05°26'N, 54°24'W

Collection date.—3 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps were placed along the edge of a dense tropical lowland forest. It was impossible to enter the forest, so traps were placed among the piles of dirt and fallen trees along the road.

Genera present.—*Oryzomys*, *Proechimys*

[Marowijne] Perica, 05°40'N, 54°37'W

Collection dates.—24–26 October 1981

Collectors/Preparators.—Arnold, Groen, Koop, Roberts, Toto, Williams

Site description.—Vegetation in the area was secondary forest with a dense understory. There were agricultural fields and grassy strips along the road and culverts in the area. Mist nets were placed at the forest edge, around buildings, over a small stream, and over part of a river. This site was not at 03°06'N, 54°31'W as indicated by the field collectors.

Genera present.—*Anoura*, *Artibeus*, *Carollia*, *Cormura*, *Dasypus*, *Eptesicus*, *Mesophylla*, *Micronycteris*, *Molossus*, *Neacomys*, *Noctilio*, *Philander*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Rhinophylla*, *Saccopteryx*, *Sturnira*, *Tonatia*, *Uroderma*, *Zygodontomys*

NICKERIE**[Nickerie] 3 km N Wageningen, 05°48'N, 56°41'W**

Collection date.—29 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—This area has rice fields partitioned by roads and irrigation canals. Along the roads and canals was grass and weedy vegetation.

Genus present.—*Zygodontomys*

PARA**[Para] 1/2 km N Airstrip, Zanderij, 05°28'N, 55°12'W**

Collection dates.—2–3, 7 January 1975; 20 September 1976

Collector/Preparator.—de la Fuente

Site description.—Specimens were collected from a culvert under the highway just north of the international airport.

Genera present.—*Artibeus*, *Carollia*, *Glossophaga*, *Macrophyllum*

[Para] Zanderij, 05°27'N, 55°12'W

Collection dates.—20 September 1976; 27–29 April 1980; 18–20 May 1980; 29–30 November 1981; 1 December 1981

Collectors/Preparators.—Arnold, Baker, de la Fuente, Genoways, Groen, Koop, Roberts, Seyfarth, Williams

Site description.—Some tall secondary trees remain, but most of the understory has been cleared for agricultural purposes, such as rubber production. A stream, ponds, and roadside ditches in the area were worked. Some open savannah intermixed with uncleared secondary forest with numerous trails were trapped, and mist nets were placed for collecting bats.

Genera present.—*Artibeus*, *Carollia*, *Chiroderma*, *Choeroniscus*, *Chrotopterus*, *Cormura*, *Desmodus*, *Eptesicus*, *Glossophaga*, *Holochilus*, *Lonchophylla*, *Marmosa*, *Mesophylla*, *Micoureus*, *Micronycteris*, *Molossus*, *Monodelphis*, *Myotis*, *Nectomys*, *Oecomys*, *Oligoryzomys*, *Peropteryx*, *Philander*, *Phylloderma*, *Phyllostomus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Saccopteryx*, *Sturnira*, *Tonatia*, *Trachops*, *Vampyressa*, *Zygodontomys*

[Saramacca] Acarani Creek, Bigi Poika, 05°25'N, 55°30'W

Collection dates.—17–18 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Mist nets were placed across Acarani Creek to capture bats.

Genera present.—*Desmodus*, *Molossus*, *Noctilio*, *Oryzomys*, *Rhynchonycteris*, *Trachops*

[Saramacca] Bigi Poika, 05°25'N, 55°30'W

Collection dates.—14–19 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps were placed in an area of swamp north of the town and mist nets were placed over the river in this same area. Trapping also was done in and around some of the houses in town where there was heavy, thorny vegetation.

Genera present.—*Artibeus*, *Caluromys*, *Carollia*, *Didelphis*, *Lonchophylla*, *Molossus*, *Myotis*, *Noctilio*, *Philander*, *Platyrrhinus*, *Proechimys*, *Tonatia*, *Trachops*, *Zygodontomys*

[Saramacca] along Coesewijne River, 4 km S, 12 km W Bigi Poika, 05°22'N, 55°37'W

Collection date.—15 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps were placed in tropical riparian forest with large trees along the edge of the Coesewijne River.

Genus present.—*Proechimys*

[Saramacca] 4 km S, 6 km W Bigi Poika, 05°22'N, 55°34'W

Collection date.—15 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps were placed in low tropical forest, in a savannah area, and in the forest-savannah ecotone.

Genera present.—*Oryzomys*, *Proechimys*, *Zygodontomys*

[Saramacca] 5 km S, 3 1/2 km W Bigi Poika, 05°21'N, 55°33'W

Collection date.—17 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Traps were placed in two vegetation types at this locality. Some traps were placed in an area of heavy secondary growth and others were placed in a forested area.

Genus present.—*Oryzomys*

[Saramacca] 5 km S, 2 km W Bigi Poika, 05°21'N, 55°32'W

Collection date.—18 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Mist netting was done in and around the Coesewijne Savannah. Nets were placed in the savannah, in cleared net lanes in the adjoining forest, across the road, and over a large pond.

Genera present.—*Ametrida*, *Artibeus*, *Rhinophylla*

[Saramacca] 5 km S Bigi Poika, 05°21'N, 55°31'W

Collection date.—16 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Work was done in an area of mixed savannah associated with swamp.

Genus present.—*Zygodontomys*

[Saramacca] 6 km S, 14 km E Bigi Poika, 05°20'N, 55°23'W

Collection date.—September 1976

Collectors/Preparators.—Merton, Williams

Site description.—Only a pick-up partial skull of a capybara obtained at this site.

Genus present.—*Hydrochaeris*

[Saramacca] 12 km S, 1 km W Bigi Poika, 05°19'N, 55°31'W

Collection date.—24 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—One road-killed opossum obtained at this place.

Genus present.—*Didelphis*

[Saramacca] approximately 15 km N, 35 km E Bitagron [= Witagron], 05°18'N, 55°44'W

Collection date.—21 November 1981

Collectors/Preparators.—Branan, Groen

Site description.—A single specimen of *Tamandua*, which was a gift from W. V. Branan, was taken at this place.

Genus present.—*Tamandua*

[Saramacca] 5 km N, 23 km W Kwakoeegron, 05°18'N, 55°33'W

Collection date.—2 September 1979

Collector/Preparator.—Williams

Site description.—A male *Saguinus midas* was hit and killed by a car as it crossed the road at this point.

Genus present.—*Saguinus*

[Suriname] Powaka [= Powakka], 05°27'N, 55°05'W

Collection dates.—30 April 1966; 23–24 September 1966; 4, 6–7 January 1975; 12, 14 September 1976; 30 July 1977; 9–11 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—This is an area of mixed habitats, including high, dense secondary gallery forest with light to moderate undergrowth, swamp, savannah, and a stream. Collecting was done in all available habitats.

Genera present.—*Artibeus*, *Carollia*, *Dasybus*, *Desmodus*, *Didelphis*, *Glossophaga*, *Lonchophylla*, *Metachirus*, *Micronycteris*, *Mimon*, *Myotis*, *Neacomys*, *Nectomys*, *Oryzomys*, *Philander*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Rhinophylla*, *Saguinus*, *Sturnira*, *Uroderma*, *Zygodontomys*

[Suriname] 1 km S, 2 km E Powaka [= Powakka], 05°25'N, 55°04'W

Collection dates.—10–11 August 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—The team placed 10 mist nets in this area of savannah and forest. The savannah had scattered shrubbery. The forest was mostly secondary growth.

Genera present.—*Ametrida*, *Artibeus*, *Carollia*, *Chiroderma*, *Molossops*, *Platyrrhinus*, *Rhinophylla*, *Uroderma*, *Vampyressa*

PARAMARIBO**[Paramaribo] Charlesburg, 2 km NNW Paramaribo, 05°51'N, 55°11'W**

Collection dates.—17 August 1966; 3 January 1975

Collector/Preparator.—de la Fuente

Site description.—No notes available.

Genera present.—*Carollia*, *Platyrrhinus*, *Saimiri*

[Paramaribo] Keizerstraat 230, Paramaribo, 05°50'N, 55°10'W

Collection dates.—9–10 January 1975

Collector/Preparator.—de la Fuente

Site description.—This location is a street address in the city of Paramaribo. Specimens were collected from an old wooden frame house.

Genera present.—*Eptesicus*, *Molossus*

[Paramaribo] Keizerstraat 232, Paramaribo, 05°50'N, 55°10'W

Collection dates.—30 December 1974; 1 January 1975

Collector/Preparator.—de la Fuente

Site description.—This location is a street address in the city of Paramaribo. Collecting was done in a flower garden surrounded by fruit trees.

Genera present.—*Artibeus*, *Glossophaga*, *Phyllostomus*

[Paramaribo] Paramaribo, 05°50'N, 55°10'W

Collection dates.—28 May 1966; 28 July 1966; 15 August 1966; 2 October 1966; 30 December 1974; 1, 9–10, 12 January 1975; 18–19 September 1976; 3, 7 July 1977; 1 August 1977; 14 August 1979; 7 October 1979

Collectors/Preparators.—de la Fuente, Groen, Honeycutt, Williams

Site description.—Collecting was done within the city of Paramaribo in gardens, orchards, around homes, and among small stands of native vegetation associated with rivers and canals.

Genera present.—*Artibeus*, *Carollia*, *Didelphis*, *Eptesicus*, *Eumops*, *Glossophaga*, *Molossus*, *Mus*, *Phyllostomus*, *Promops*, *Rattus*

[Suriname] Paramaribo, 05°49'N, 55°10'W

Collection dates.—18 October 1981; 9 November 1981; 19 November 1981

Collectors/Preparators.—Arnold, Genoways, Groen, Koop, Phillips, Toto, Williams

Site description.—Mist nets were placed in the vicinity of a pond and canal on the campus of the University of Suriname. The canal was bordered by ornamental trees.

Genera present.—*Artibeus*, *Eptesicus*, *Glossophaga*, *Lasiurus*, *Molossus*, *Myotis*, *Noctilio*, *Saccopteryx*

[Suriname] Plantation Clevia, 8 km NE Paramaribo, 05°52'N, 55°08'W

Collection dates.—18 October 1981; 1 November 1981; 8–10 November 1981

Collectors/Preparators.—Arnold, Genoways, Groen, Honeycutt, Koop, Phillips, Williams

Site description.—This was an area of sugarcane fields and other agricultural lands. Traps were placed in the grass and shrubs associated with terraces in the agricultural fields. Some traps also were placed in a small, private orchard.

Genera present.—*Holochilus*, *Philander*, *Zygodontomys*

[Suriname] 7 km NE Paramaribo, 05°52'N, 55°07'W

Collection date.—17 October 1981

Collector/Preparator.—Williams

Site description.—A single road-killed *Procyon* was preserved from this place.

Genus present.—*Procyon*

SARAMACCA

[Saramacca] 5 km N, 30 km W Groningen, 05°46'N, 55°51'W

Collection date.—28 September 1981

Collectors/Preparators.—Branan, Williams

Site description.—A single specimen of *Lontra*, which was a gift from W. V. Branan, was taken at this place.

Genus present.—*Lontra*

SIPALIWINI

[Brokopondo] 1 km N Rudi Kappelvliet, 300 m, 03°48'N, 56°09'W

Collection dates.—28–30 September 1979; 3 October 1979

Collectors/Preparators.—Genoways, Groen, Honeycutt, Phillips, Roberts, Williams

Site description.—This location is in the Tafelberg Nature Preserve in central Suriname. This site is at the end of a wide, cleared, grassy path leading to the water tower and stream that is the source of water for the local residents. Large buttress-rooted trees form the border of the path with the largest trees near the stream. The general vegetation of the area was virgin lowland and lower montane rainforest.

Genera present.—*Ametrida*, *Anoura*, *Artibeus*, *Carollia*, *Lonchophylla*, *Micronycteris*, *Neacomys*, *Nectomys*, *Phyllostomus*, *Potos*, *Proechimys*, *Rhinophylla*, *Tonatia*, *Uroderma*

[Brokopondo] 1 1/2 km W Rudi Kappelvliet, 330 m, 03°47'N, 56°10'W

Collection dates.—2–4 October 1979

Collectors/Preparators.—Genoways, Groen, Honeycutt, Phillips, Roberts, Williams

Site description.—This location is in the Tafelberg Nature Preserve in central Suriname. Mist nets were placed along a trail in an area of immature tropical forest with a moderate understory.

Genera present.—*Artibeus*, *Carollia*, *Marmosa*, *Micronycteris*, *Oryzomys*, *Phyllostomus*, *Proechimys*, *Thyroptera*, *Tonatia*, *Trachops*, *Vampyressa*, *Zygodontomys*

[Brokopondo] Rudi Kappelvliegveld, 320 m, 03°47'N, 56°09'W

Collection dates.—26–30 September 1979; 1–4 October 1979; 6 November 1981

Collectors/Preparators.—Genoways, Groen, Honeycutt, Phillips, Roberts, Williams

Site description.—This location is in the Tafelberg Nature Preserve in central Suriname. This is the location of the airstrip, which is in an extensive natural savannah with a fringing mature tropical lowland rainforest. There were a few buildings associated with the airport and nearby residences.

Genera present.—*Ametrida*, *Artibeus*, *Carollia*, *Cebus*, *Eptesicus*, *Glossophaga*, *Molossus*, *Nectomys*, *Noctilio*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Sturnira*, *Uroderma*, *Vampyrum*, *Zygodontomys*

[Brokopondo] 3 km SW Rudi Kappelvliegveld, 320 m, 03°46'N, 56°10'W

Collection dates.—1–2, 4 October 1979

Collectors/Preparators.—Genoways, Groen, Honeycutt, Phillips, Roberts, Williams

Site description.—This location is in the Tafelberg Nature Preserve in central Suriname. Work was conducted in a mature lowland tropical rainforest with a moderate understory. This understory was cleared to create a lane for the placement of mist nets. During one night mist nets were placed in an area where the dominant tree was mountain palm. There was no stream in the general area.

Genera present.—*Artibeus*, *Carollia*, *Chrotopterus*, *Eptesicus*, *Lonchophylla*, *Micronycteris*, *Mimon*, *Phylloderma*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Saccopteryx*, *Tonatia*, *Trachops*, *Uroderma*, *Vampyressa*

[Marowijne] Oelemarie [or Oelemari], 03°06'N, 54°32'W

Collection dates.—20–26 November 1981

Collectors/Preparators.—Arnold, Groen, Held, Koop, Mohadin, Roberts, Williams

Site description.—The vegetation in the general area was dense tropical rainforest with a moderate understory. The airstrip and a few buildings were located in a small savannah. Work centered in the vicinity of the Oelemari River, the forest-savannah ecotone, and in the rainforest.

Genera present.—*Agouti*, *Ametrida*, *Artibeus*, *Carollia*, *Centronycteris*, *Chrotopterus*, *Dasyprocta*, *Eptesicus*, *Lonchophylla*, *Lonchorhina*, *Makalata*, *Marmosa*, *Micronycteris*, *Mimon*, *Molossus*, *Monodelphis*, *Myoprocta*, *Myotis*, *Neacomys*, *Nectomys*, *Noctilio*, *Oecomys*, *Oryzomys*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Rhynchonycteris*, *Saccopteryx*, *Sciurus*, *Sturnira*, *Tonatia*, *Uroderma*

[Nickerie] 24 km S, 60 km E Apoera, 04°57'N, 56°35'W

Collection dates.—5–6 September 1979

Collectors/Preparators.—Groen, Honeycutt, Roberts, Williams

Site description.—Vegetation at this site consisted of a dense pioneer community along the roadside that graded into an old second growth forest. Mist nets were placed across the road, over a nearby river, over a bridge, and across trails in the secondary forest. This site was not at 04°41'N, 56°07'W as indicated by the field collectors.

Genera present.—*Artibeus*, *Carollia*, *Lonchophylla*, *Myotis*, *Neacomys*, *Noctilio*, *Phyllostomus*, *Proechimys*, *Rhinophylla*, *Rhynchonycteris*, *Sturnira*, *Vampyressa*

[Nickerie] 26 km S, 55 km E Apoera, 04°56'N, 56°38.5'W

Collection date.—22 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Mist nets and traps were placed in the forest in the vicinity of Moses Creek.

Genera present.—*Artibeus*, *Carollia*, *Chiroderma*, *Platyrrhinus*, *Proechimys*, *Rhynchonycteris*, *Sturnira*

[Nickerie] 35 km S, 5 km E Apoera, 04°51'N, 57°07'W

Collection date.—23 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—The dense tropical forest and a river were the sites for traps and mist nets.

Genera present.—*Carollia*, *Mazama*, *Myotis*, *Proechimys*, *Rhinophylla*, *Sturnira*

[Nickerie] 38 km S, 27 km E Apoera, 04°50'N, 56°56'W

Collection date.—24 July 1977

Collectors/Preparators.—de la Fuente, Williams

Site description.—Collecting was done in dense tropical forest, a small garden with bananas and squash, and some small open grassy areas.

Genera present.—*Neacomys*, *Proechimys*

[Nickerie] Avanavero, 04°50'N, 57°14'W

Collection dates.—24–27 May 1980

Collectors/Preparators.—Groen, Roberts, Seyfarth, Williams

Site description.—Work was conducted in old secondary tropical forest. Considerable clearing of forest was being done in the general vicinity in preparation for the construction of a new dam.

Genera present.—*Ametrida*, *Artibeus*, *Carollia*, *Cormura*, *Glossophaga*, *Lonchophylla*, *Lonchorhina*, *Marmosa*, *Micronycteris*, *Molossus*, *Monodelphis*, *Nectomys*, *Oecomys*, *Philander*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Sturnira*, *Tonatia*, *Uroderma*, *Vampyrodes*

[Nickerie] Grassalco, 04°46'N, 56°48'W

Collection dates.—7–8 September 1979

Collectors/Preparators.—Groen, Honeycutt, Roberts, Williams

Site description.—This location was in a river valley filled with secondary tropical forest. Collecting was done along trails through the forest and along the river.

Genera present.—*Anoura*, *Artibeus*, *Carollia*, *Chiroderma*, *Choeroniscus*, *Lionycteris*, *Lonchophylla*, *Molossops*, *Molossus*, *Myotis*, *Neacomys*, *Noctilio*, *Philander*, *Phylloderma*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Rhynchonycteris*, *Sturnira*, *Tonatia*, *Vampyressa*

[Nickerie] Kabalebo, 04°25'N, 57°13'W

Collection dates.—28–30 May 1980

Collectors/Preparators.—Groen, Roberts, Seyfarth, Williams

Site description.—This is an area of low rolling hills covered with a mixed secondary and primary lowland rainforest. Considerable clearing of forest was being done in the general vicinity in preparation for the construction of a new dam. This site is not at 04°51'N, 57°24'W as indicated by the field collectors.

Genera present.—*Artibeus*, *Carollia*, *Glossophaga*, *Lonchophylla*, *Micronycteris*, *Nectomys*, *Oryzomys*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Saccopteryx*, *Sturnira*, *Tonatia*, *Trachops*, *Uroderma*

[Nickerie] Kayserberg Airstrip, 03°06'N, 56°28'W

Collection dates.—30 April 1980; 1–6 May 1980

Collectors/Preparators.—Groen, Roberts, Seyfarth, Williams

Site description.—Located in the Eilerts de Haan Nature Preserve along the Zuid River in a valley between the Eilerts de Haan Mountains and Kayser Mountains. The area was covered in mature lowland rainforest.

Genera present.—*Alouatta*, *Ametrida*, *Artibeus*, *Ateles*, *Carollia*, *Cebus*, *Dasyprocta*, *Eptesicus*, *Glossophaga*, *Lonchophylla*, *Micronycteris*, *Molossus*, *Monodelphis*, *Myotis*, *Oecomys*, *Pecari*, *Philander*, *Phyllostomus*, *Proechimys*, *Pteronotus*, *Saccopteryx*, *Sturnira*, *Tonatia*, *Trachops*, *Uroderma*, *Zygodontomys*

[Nickerie] Sipaliwini Airstrip, 02°02'N, 56°08'W

Collection dates.—16–21 August 1979; 11–18 November 1981

Collectors/Preparators.—Arnold, Groen, Honeycutt, Koop, Reichert, Roberts, Williams

Site description.—The airstrip was located in a large natural savannah surrounded by dense lowland tropical forest. Some of the forest was tall, with buttressed roots, but dense secondary vegetation dominated in some areas. The Sipaliwini River ran nearby with a well-developed gallery forest.

Genera present.—*Anoura*, *Artibeus*, *Ateles*, *Bradypus*, *Carollia*, *Cavia*, *Cebus*, *Chiropotes*, *Choeroniscus*, *Chrotopterus*, *Dasyprocta*, *Eptesicus*, *Glossophaga*, *Holochilus*, *Hydrochaeris*, *Lasiurus*, *Lonchophylla*, *Marmosa*, *Mazama*, *Mesophylla*, *Micoureus*, *Micronycteris*, *Molossops*, *Molossus*, *Myotis*, *Natalus*, *Neacomys*, *Odocoileus*, *Oecomys*, *Oligoryzomys*, *Pecari*, *Philander*, *Phylloderma*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Rhogeessa*, *Rhynchonycteris*, *Saimiri*, *Sigmomys*, *Sturnira*, *Tayassu*, *Thyroptera*, *Tonatia*, *Trachops*, *Uroderma*, *Zygodontomys*

[Nickerie] 1 km S, 3.5 km E Sipaliwini Airstrip, 02°01'N, 56°06'W

Collection date.—19 August 1979

Collectors/Preparators.—Groen, Honeycutt, Roberts, Williams

Site description.—Work was done in a natural savannah and the riverine forest along a small stream. There were a few trees scattered in the savannah.

Genera present.—*Artibeus*, *Glossophaga*, *Lasiurus*, *Lionycteris*, *Saccopteryx*, *Trachops*

[Saramacca] Bitagron [= Witagron], 05°10'N, 56°06'W

Collection dates.—3–4 September 1979

Collectors/Preparators.—Groen, Honeycutt, Roberts, Williams

Site description.—Habitats at this location were dominated by dense secondary forest with fringing shrubbery and grass. Some work was done in a “garden” containing banana and coconut trees. This site is not at 05°06'N, 56°04'W as indicated by the field collectors.

Genera present.—*Artibeus*, *Carollia*, *Lonchophylla*, *Philander*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Rhinophylla*, *Sturnira*, *Tonatia*

[Saramacca] N rim of Arrowhead Basin, Tafelberg, 725 m, 03°55'N, 56°10'W

Collection date.—2 November 1981

Collector/Preparator.—Groen

Site description.—The collecting site was on the top of Tafelberg (600 m), which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve. This area was a large, barren granite shield surrounded by tropical bush. The only plants on the granite shield were located along large crevices where small amounts of soil had accumulated. All of these plants were low in form and included grasses, cacti, small shrubs, and orchids.

Genus present.—*Proechimys*

[Saramacca] N side of Arrowhead Basin, Tafelberg, 600 m, 03°55'N, 56°10'W

Collection date.—4 November 1981

Collectors/Preparators.—Groen, Koop

Site description.—The collecting site was in the large basin on the top of Tafelberg, which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve. In the basin, the forest is dominated by dakama (*Dimorphandra* sp.) with large buttressed roots, forming a dense canopy that allowed only filtered light to reach the ground. Traps were set along the steep cliffs and among the fallen rocks along the northern side of the basin.

Genus present.—*Proechimys*

[Saramacca] Center of Arrowhead Basin, Augustus Creek, Tafelberg, 600 m, 03°54'N, 56°10'W

Collection dates.—2–4 November 1981

Collectors/Preparators.—Groen, Roberts, Williams

Site description.—The collecting site was in the center of a large basin on the top of Tafelberg, which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve. In the basin, the forest is dominated by dakama (*Dimorphandra* sp.) with large buttressed roots, forming a dense canopy that allowed only filtered light to reach the ground. Traps were placed among the logs and the rocks that bordered the stream. Mist nets were placed across Augustus Creek and its small tributaries and into the adjoining forest. One group of nets was placed over a dry pond in an opening in the forest.

Genera present.—*Artibeus*, *Carollia*, *Eptesicus*, *Neacomys*, *Oryzomys*, *Proechimys*, *Pteronotus*, *Rhinophylla*

[Saramacca] SE side of Arrowhead Basin, Augustus Creek, Tafelberg, 600 m, 03°54'N, 56°10'W

Collection dates.—31 October 1981; 1–2 November 1981

Collectors/Preparators.—Groen, Williams

Site description.—The collecting site was in the center of a large basin on the top of Tafelberg (600 m), which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve. In the basin, the forest is dominated by dakama (*Dimorphandra* sp.) with large buttressed roots, forming a dense canopy that allowed only filtered light to reach the ground. Traps were set along the edge of Augustus Creek, and mist nets were

placed in the forest habitat and across the creek where there were isolated ponds among the boulders.

Genera present.—*Anoura*, *Artibeus*, *Carollia*, *Eptesicus*, *Glossophaga*, *Micronycteris*, *Myotis*, *Oryzomys*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Saccopteryx*, *Sturnira*, *Tonatia*

[Saramacca] Lower Geyskes Creek, Tafelberg, 600 m, 03°56'N, 56°11'W

Collection dates.—4–5 November 1981

Collectors/Preparators.—Arnold, Genoways, Groen, Koop, Phillips, Roberts, Williams

Site description.—The collecting site was on the top of Tafelberg (600 m), which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve. The forest along the stream and adjacent areas was dominated by dakama (*Dimorphandra* sp.) with large buttressed roots. Beyond these trees were areas of tropical bush and some open savannah. The stream consisted of several large, deep pools in this area.

Genera present.—*Ametrida*, *Anoura*, *Artibeus*, *Carollia*, *Chiroderma*, *Eptesicus*, *Neacomys*, *Oryzomys*, *Proechimys*, *Rhinophylla*, *Tonatia*, *Vampyressa*

[Saramacca] Geyskes Creek, Tafelberg, 700 m, 03°56'N, 56°10'W

Collection dates.—29–31 October 1981; 3–4 November 1981

Collectors/Preparators.—Arnold, Genoways, Groen, Koop, Phillips, Roberts, Williams

Site description.—The main base camp for work on Tafelberg was situated here along Geyskes Creek. The creek was intermittent at this point with some areas of running water, some pools of water, and some dry areas. The area along the creek was very rocky, with boulder-sized rocks at many points. Most of the top of the mountain was dominated by intermediate tropical bush with relatively short trees with a heavy undergrowth, but along the stream the forest was higher with buttress-rooted trees. The collecting site was on the top of Tafelberg, which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve.

Genera present.—*Ametrida*, *Artibeus*, *Carollia*, *Chiroderma*, *Glossophaga*, *Myotis*, *Oryzomys*, *Phyllostomus*, *Proechimys*

[Saramacca] Geyskes Creek, Tafelberg, 700 m, 03°55'N, 56°10'W

Collection dates.—1–5 November 1981

Collectors/Preparators.—Arnold, Genoways, Groen, Koop, Phillips, Roberts, Williams

Site description.—A place near the main base camp with similar habitats and collecting situations. The collecting site was on the top of Tafelberg (600 m), which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve.

Genera present.—*Artibeus*, *Carollia*, *Chiroderma*, *Glossophaga*, *Neacomys*, *Oryzomys*, *Platyrrhinus*, *Proechimys*, *Rhinophylla*

[Saramacca] Upper Geyskes Creek, Tafelberg, 775 m, 03°55'N, 56°10'W

Collection dates.—5 November 1981

Collectors/Preparators.—Arnold, Genoways, Groen, Koop, Phillips, Roberts, Williams

Site description.—Work was done in an open savannah-type habitat along the creek. Tropical bush surrounded the open area. The collecting site was on the top of Tafelberg (600 m), which is the eastern-most tepui, or flat-topped, Cretaceous sandstone mountain

overlaying the ancient pre-Cambrian Guyana Crystalline Shield, within the Tafelberg Nature Preserve.

Genera present.—*Neacomys*, *Proechimys*

[Saramacca] Raleigh Falls, 04°43'N, 56°12'W

Collection dates.—24–30 August 1979; 10, 14–15 May 1980

Collectors/Preparators.—Baker, Genoways, Groen, Honeycutt, Roberts, Seyfarth, Williams

Site description.—This collecting site is on an island in the Coppename River in the Raleigh Vallen Nature Preserve. Relatively dense, near-mature tropical lowland forest with only a limited understory occupied most of the area. The largest tropical trees were located near the banks of the Coppename River.

Genera present.—*Ametrida*, *Artibeus*, *Carollia*, *Chiroderma*, *Chrotopterus*, *Cormura*, *Desmodus*, *Lonchophylla*, *Marmosa*, *Micronycteris*, *Molossus*, *Monodelphis*, *Myotis*, *Nectomys*, *Noctilio*, *Oecomys*, *Oryzomys*, *Philander*, *Phylloderma*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Rhynchonycteris*, *Saccopteryx*, *Sturnira*, *Thyroptera*, *Tonatia*, *Trachops*, *Uroderma*, *Vampyroides*

[Saramacca] Voltzberg, 04°40'N, 56°12'W

Collection dates.—28 August 1979; 11–13 May 1980

Collectors/Preparators.—Baker, Genoways, Groen, Honeycutt, Roberts, Seyfarth, Williams

Site description.—This collecting site is in the Raleigh Vallen Nature Preserve. The Voltzberg is a huge outcrop of nearly bare granite. Numerous small caves and crevices were formed along its perimeter. The forest surrounding the Voltzberg was virgin tropical rainforest. A small stream ran through the area near the campsite.

Genera present.—*Anoura*, *Artibeus*, *Carollia*, *Desmodus*, *Didelphis*, *Furipterus*, *Glossophaga*, *Lonchophylla*, *Marmosa*, *Micronycteris*, *Mimon*, *Peropteryx*, *Philander*, *Phylloderma*, *Phyllostomus*, *Platyrrhinus*, *Proechimys*, *Pteronotus*, *Rhinophylla*, *Saccopteryx*, *Tonatia*, *Trachops*

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ASPIDOSAURUS BINASSER (AMPHIBIA, TEMNOSPONDYLI), A NEW SPECIES OF DISSOROPHIDAE FROM THE LOWER PERMIAN OF TEXAS

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ABSTRACT

A new species of the dissorophid amphibian *Aspidosaurus*, *A. binasser*, is based on a single specimen consisting of the greater part of the skull and short, articulated strings of vertebrae, as well as numerous isolated and fragmentary vertebrae, from the presacral and caudal regions of the column collected from the Lower Permian (Leonardian) Arroyo Formation, Clear Fork Group, Baylor County, Texas. Comparisons with the holotype and only known specimen of the type species, *A. chiton* Broili, 1904, also from the Arroyo Formation in Texas and consisting not only of small portions of the vertebral column, but the only previously known skull of the genus, is unfortunately limited because it was lost during World War II. Although numerous characters of the skulls of *A. binasser* and *A. chiton* clearly document a dissorophid assignment, only one unique character is recognized that both share among the dissorophids, a relatively long preorbital skull length. The skull of *A. binasser* possesses a number of unique characters, as well as a combination of characters, that distinguish it from other dissorophids. These offer a better understanding of *Aspidosaurus* that dispels speculation of a closer relationship with *Platyhystrix* than with any other dissorophid.

Although the armored neural spines of *A. binasser* are *Aspidosaurus*-like in their fundamental structural plan, they exhibit a wide range of morphologies heretofore unknown in the genus, including two variants that distinguish it from *A. chiton* and the only other described species of *Aspidosaurus*, *A. glascocki* Case, (1910), *A. apicalis* (Cope, 1878), and *A. crucifer* (Case, 1903). The latter are regarded here as *nomina dubia*, as their holotypes, consisting of very small, isolated portions of the vertebral column from the Lower Permian of Texas and New Mexico, are considered insufficient for species identification.

KEY WORDS: Dissorophidae (*Aspidosaurus*), Temnospondyli, vertebral armor, Lower Permian, Texas

INTRODUCTION

Since its first use, the constitution of Dissorophidae Boulenger, 1902, has received numerous revisions. The early history of these revisions has been chronicled by DeMar (1966) in a detailed review of the early taxonomic history and relationships of the group. Recent phylogenetic studies (Boy, 1972; Dilkes, 1990; Daly, 1994) have tended to restrict Dissorophidae to its highly terrestrial genera, almost all of which are known to possess the specialization of well-developed, sculptured, dermal armor segments closely associated with the neural spines of the vertebral column. Unarmored genera, such as *Amphibamus*, *Doleserpeton*, and *Tersomius*, originally included in Dissorophidae, have been reassigned (Daly, 1994; Boy, 1972) to Amphibamidae (erected by Boy, 1972, solely for *Amphibamus*), although remaining united with Dissorophidae under Dissorophoidea. Daly (1994) proposed a further breakup of the Dissorophidae, viewing the somewhat aberrant *Platyhystrix*, *Astreptorhachis*, and *Ecolsonia* as deserving of separate family status, despite being considered dissorophids by most authors (Vaughn, 1971; Berman et al., 1981, 1985), uniting the first two in the new family Platyhystricidae, while judging the family status of

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Ecolsonia as unresolved and best left as *incertae sedis*. With the exception of Daly's suggested classification, Dissorophidae represents one of the largest groups of Paleozoic temnospondyl amphibians, including about 16 genera, having a temporal and spatial range from the Late Pennsylvanian and Early Permian of the United States (Carroll, 1964; Vaughn, 1971; Berman and Berman, 1975; Berman et al., 1985) to the Late Permian of Russia (Eichwald, 1848; Gubin, 1980) and China (Li and Cheng, 1999). In addition, vertebrae described and referred to *Actinodon* by Gaudry (1879, 1883) from the Late Carboniferous of France were recognized by Romer (1947) as being of the aspidosaur type.

It is undoubtedly the conspicuous armor that most dramatically characterizes the Dissorophidae. In a detailed phylogenetic and functional analysis of the armor of dissorophids, DeMar (1966, 1968) concluded that it served several functions, all directly related to a highly terrestrial existence. Although primarily a means of strengthening and restricting movements of the vertebral column, secondary functions of the armor probably included reduction of water loss by evaporation through the skin and protection from predators. Most importantly, the armor has also been a major source of data for taxonomic and phylogenetic considerations of dissorophids (Carroll, 1964; DeMar, 1966, 1968; Bolt, 1974). DeMar's (1966, 1968) studies of dissorophid armor not only demonstrated a wide range in gross and detailed morphologies between most species, but the presence of distinct structural patterns that indicate the independent development of armor in at least two, possibly three, different lines during the Late Pennsylvanian or Early Permian.

One of the least understood of all the armored dissorophids is *Aspidosaurus*. Several circumstances account for this. The holotype and only known specimen of the type species, *A. chiton* Broili, 1904, consists of the greater portion of the skull and small portions of the armored vertebral column from a single site, Coffee Creek, in the Lower Permian Arroyo Formation of Texas. The skull and vertebrae were cataloged separately at the Museum of the Alte Akademie, Munich, as nos. 84 and 85, respectively, even though they were apparently regarded as belonging to a single individual. Unfortunately, the holotype was lost during World War II and therefore has not been available for recent comprehensive studies of Dissorophidae (Carroll, 1964; DeMar, 1966, 1968). Broili's (1904) description of the holotype, however, has remained sufficient to accept the validity of *A. chiton* and its dissorophid assignment. Undoubtedly, it has been in large part the character of the vertebrae, or more specifically the dermal armor capping the neural spines, that has had the greatest influence in the continued recognition of *A. chiton* as a dissorophid.

In general, the armor consists of small, coarsely sculptured, transversely narrow, roof-shaped pieces of dermal bone that are fused firmly to and slope ventrolaterally from the dorsal surface of the distally expanded neural spine and that may or may not overlap each other along their anterior and posterior margins (Carroll, 1964; DeMar, 1966). Although Broili's (1904) illustrations indicate two or three varieties of armored neural spines in *A. chiton*, his description and generalized reconstruction of two articulated presacral vertebrae with slightly overlapping armor segments apparently misled later workers (Case, 1911; DeMar, 1966) into believing that they characterize the entire column. As a further source of confusion, three additional species of *Aspidosaurus* have been described, all based on very small portions of the armored vertebral column from the Lower Permian of Texas and New Mexico: *A. glascocki* Case (1910), *A. apicalis* (Cope, 1878), and *A. crucifer* (Case, 1903). Whereas all three species assuredly belong to *Aspidosaurus*, the incompleteness of the holotypes and the very modest differences they exhibit between not only each other but with *A. chiton* as well, strongly suggests that only the latter is valid.

A recently discovered specimen of *Aspidosaurus* from the Lower Permian Arroyo Formation of Texas (Fig. 1) is described here as a new species. It consists of the greater part of the skull and short, articulated strings of vertebrae, as well as numerous isolated and

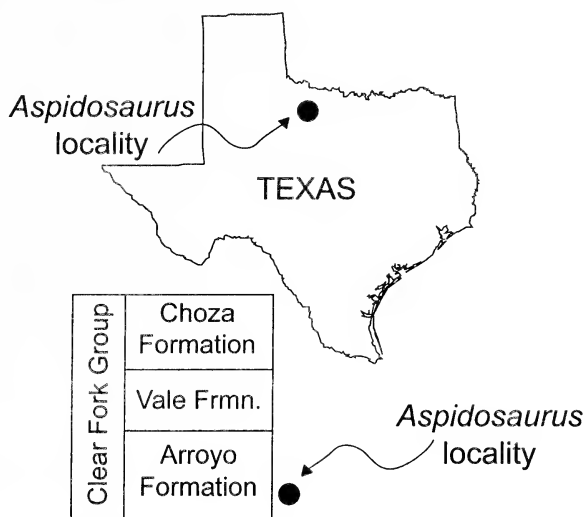


Fig. 1.—Locality map and generalized stratigraphic section of Lower Permian Clear Fork Group showing location of the holotype of *Aspidosaurus binasser*, TMM 43531-1.

fragmentary vertebrae, from the presacral and caudal regions. As far as can be determined from Broili's (1904) description, the skull appears to be identical to that of *A. chiton*, sharing with it not only several dissorophid characters, but also one that is unique among dissorophids, a relatively long preorbital region of the skull. Equally significant, although the armored neural spines of the new species are undeniably *Aspidosaurus*-like in their basic structural plan, they exhibit a range of morphologies heretofore not suspected in any of the previously described species of *Aspidosaurus*, including two variants that are unique.

The following acronyms are used to refer to institutional repositories of specimens: AMNH, American Museum of Natural History, New York, New York; CNMH, Chicago Natural History Museum, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; TMM, Texas Memorial Museum, University of Texas, Austin.

Anatomical structures are identified by the following abbreviations: apf, anterior palatal fenestra; bo, basioccipital; ex, external naris; f, frontal; in, internal naris; inf, internarial fenestra; j, jugal; l, lacrimal; m, maxilla; n, nasal; oc, occipital condyle; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal; prf, prefrontal; ps, parasphenoid; psp, postsphenial; pt, pterygoid; s, stapes; scp, sclerotic plates; sm, septomaxilla; sp, splenial; sq, squamosal; st, supratemporal; t, tabular; ts, tusk or tusk and socket pair.

SYSTEMATIC PALEONTOLOGY

Order Temnospondyli Zittel, 1888

Superfamily Dissorophoidea Bolt, 1969

Family Dissorophidae Boulenger, 1902

Genus *Aspidosaurus* Broili, 1904

Type species *Aspidosaurus chiton* Broili, 1904

Diagnosis.—Large dissorophid temnospondyl distinguished by the following unique cranial characters: 1) preorbital skull length 51 to 54% of the midline skull length and

significantly greater than the postorbital length; 2) maxilla and its dentition extend posteriorly to a level just posterior to the anterior margin of orbit; 3) nasal and lacrimal margins of external naris are beveled ventrally to a sharp edge that appears serrated due to the dorsal surface sculpturing; 4) frontals extend anteriorly to a level well beyond the orbits and equal to the anterior extent of the prefrontals; 5) jugal extends anteriorly to approximately the level of the anterior margin of the orbit; 6) presence of an anterior palatal fenestra. The following cranial features collectively distinguish *Aspidosaurus* from other dissorophids: 1) exposure of palatine on skull roof; 2) presence of an internarial fenestra or median rostral fontanel; 3) internal naris extremely long, with a length three times its width; 4) basipterygoid process of braincase and basal process of pterygoid firmly united suturally in an immobile basicranial articulation.

The armored neural spines (defined here as the endochondral vertebral neural spine plus the dermal bone segment or armor capping it) may vary widely in morphology but exhibit a single general structural pattern: each coarsely sculptured, small, transversely and longitudinally narrow, roof-shaped dermal bone segment or armor is firmly fused to the dorsal surface of the distally expanded neural spine so that roof halves slope ventrolaterally. The armored neural spines are not partially overlapped by a second, more superficial set of segmental plates of dermal bone.

Remarks.—Although Broili's (1904) emphasis on the description of the axial skeleton in *A. chiton* provides a strong basis for identification, his description of the skull offered little more than the establishment of its dissorophid affinities. The holotypes of the only other known species of *Aspidosaurus*, *A. glascocki*, *A. apicalis*, and *A. crucifer*, are based on fragmentary postcranial specimens consisting mainly or solely of vertebrae with fused dermal armor and are here considered insufficient to permit specific identification and, thus, are regarded as *nomina dubia*. Therefore, inasmuch as the only known differences between the holotypes of *A. binasser* (TMM 43531-1) and the type species are restricted to the postcranium, cranial features of the former are used in the generic diagnosis, which is intended as a guide for comparisons with the future discoveries, with the expectation that amendments will be necessary.

Aspidosaurus binasser, new species

Holotype.—TMM 43531-1, greater portion of skull, preserved in several major pieces, and several short strings of from two to five articulated vertebrae and numerous isolated and fragmentary vertebrae from the presacral and caudal regions. There is no reason to suspect more than one individual is represented. A considerable amount of appendicular material was, however, collected along with the holotype, some too fragmentary to identify but most evidently pertaining to a pelycosaurian-grade synapsid.

Horizon and Locality.—TMM 43531-1 was collected by Mark Rowland in strata of the lower part of the Lower Permian Clear Fork Group on the north shore of Lake Kemp in Baylor County, Texas (approximately at 33°47.91' north latitude, and 99°11.34' west longitude) (Fig. 1). This locality is near the base of the Clear Fork Group, stratigraphically well below marker sandstone 4 of Hentz and Brown (1987), and approximately at the level of the "Craddock dolomite" Nelson et al. (2001), so it is in strata equivalent to the Leonardian Arroyo Formation (Hentz, 1988; Nelson et al., 2001).

Diagnosis.—Neural spines of probable presacral and anterior caudal vertebrae with prominent bilaterally paired tubercles, and neural spine and its sculptured dermal armor of probable anterior caudal vertebrae extremely compressed laterally in the form of a thin, spatulate structure.

Etymology.—Derived from the Latin *binus*, meaning two by two, couple, or pair, and *asser*, meaning beam or pole, referring to the prominent pair of bilateral tubercles on most of the neural spines of the presacral and anterior caudal vertebrae.

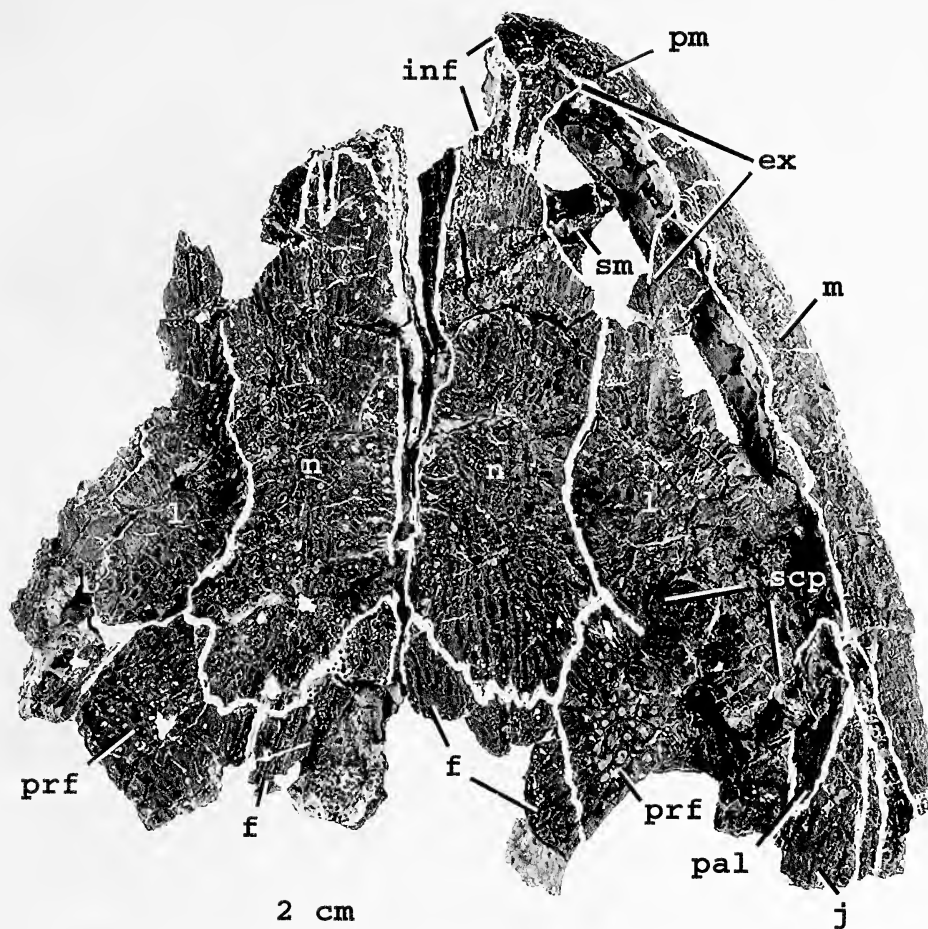


Fig. 2.—*Aspidosaurus binasser*, holotype, TMM 43531-1. Preorbital portion of skull in dorsal view.

DESCRIPTION

Skull and Lower Jaw.—The main, preserved portions of the skull include: 1) anterior portion of the skull, including the roof and palate, extending from a level at about the mid-length of the orbits (Figs. 2 and 3). Within this portion most of the losses to the skull roof and palate are areas marginal to the maxillae; 2) a disarticulated left premaxilla (Fig. 4A–C); 3) a narrow strip of the right side of the skull roof that extends from the orbit and borders the dorsal margin of the otic notch to end close to the distal end of the posterolateral, horn-like extension of the skull table and includes portions of the postfrontal, postorbital, squamosal, supratemporal, and tabular (Fig. 4D); 4) an essentially complete braincase with a partial left stapes and fragments of the overlying parietal, postparietal, and supratemporal (Fig. 5); and 5) the anterior portions of both mandibles, with the right being the most complete and including elements anterior to the adductor fossa.

The skull of *Aspidosaurus binasser* (TMM 14151-1) is unmistakingly dissorophid in structure, but does exhibit numerous features that easily distinguish it from other members of the group. The preserved, anterior portion of the skull (Figs. 2 and 3) indicates a broadly rounded snout. This portion of the skull and those including the dorsal rim of the otic notch

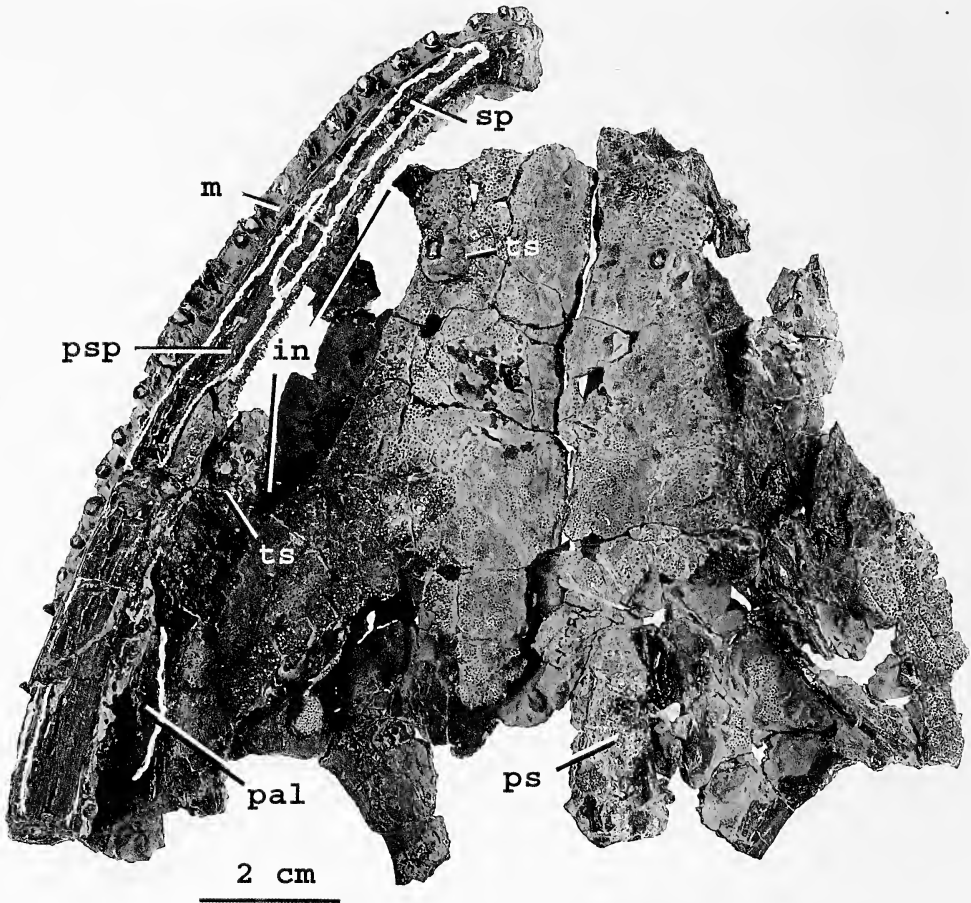


Fig. 3.—*Aspidosaurus binasser*, holotype, TMM 43531-1. Preorbital portion of skull in ventral view.

(Fig. 4D) and posterior margin of the skull table preserved with the braincase (Fig. 5) allow for fairly accurate estimates of the following pertinent skulls measurements: total length along the midline, 19.5 cm; preorbital length, 10.5 cm; postorbital length along the midline, 5.0 cm, and to the level of distal end of tabular, 7.0 cm; minimum interorbital width, 3.8 cm; longitudinal and transverse diameters of orbit, 3.0 cm. These measurements indicate a preorbital length that is nearly 54% of the midline skull length and significantly greater than the postorbital length. The pattern of the dermal sculpturing of the skull roof is typical of moderate- to large-sized dissorophids, consisting of a reticulate network of ridges surrounding deep pits or short furrows. Its greatest development is along the lateral and posterior margins of the skull table and the orbital margins, where deep, circular pits predominate, whereas its least developed is in the central, preorbital area, where a general pattern of short, shallower furrows radiate from a central area. The prefrontal and postorbital are greatly thickened into broadly rounded, anteroposteriorly oriented, ridge-like swellings that become broader and thicker toward the orbital rim.

Both premaxillae are present. The isolated left premaxilla (Fig. 5) lacks the dorsal process, whereas the right is complete, but not fully exposed, and articulated with the skull roof and forms the anterior and anterolateral margins of the external naris. Its narrow,

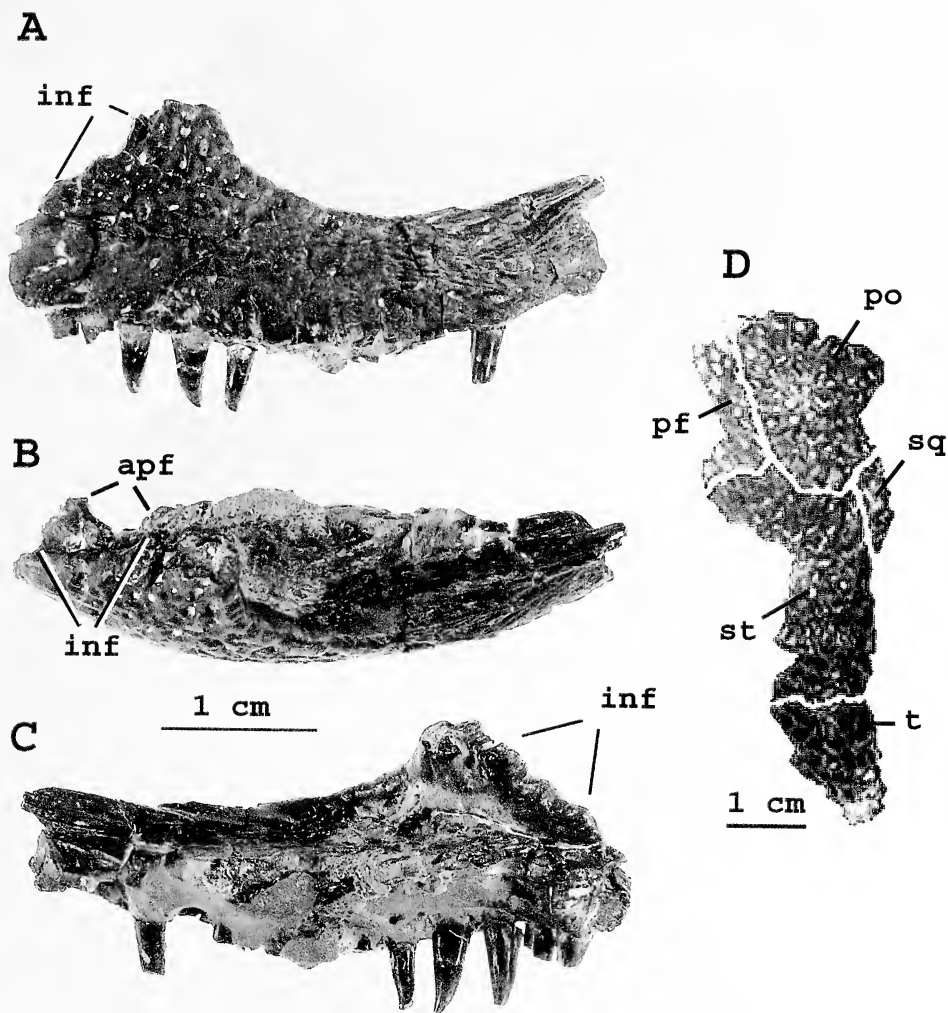


Fig. 4.—*Aspidosaurus binasser*, holotype, TMM 43531-1. Left premaxilla in A, lateral, B, dorsal, and C, medial views. D, Narrow strip of right side of the skull-roof table that extends from the orbital margin of the postorbital to nearly the distal end of the posterolateral, horn-like extension of the tabular.

rectangular, posterodorsal process projects into the anterior end of the nasal very near its narial margin. A narrow palatal shelf projects medially from about the level of the dorsal surface of the alveolar shelf. At the anterior end of the lateral margin of the shelf is a small, semicircular notch of unknown function that likely united with a similar notch on the lateral margin of the vomer. Each premaxilla possessed 13 teeth or alveoli, but only the left premaxilla retains a few complete teeth. They are sharply pointed cones with the distal ends curving slightly posteromedially. There appears to be a slight decrease in tooth size posteriorly from a basal diameter of about 4 mm and a length of about 10 mm to about 3 and 9 mm, respectively. There is no indication of “caniniform” teeth. Both nasals are essentially complete and have a narrow, rectangular outline in which the width equals about one-third the length. At the intersection of the paired premaxillae and nasals

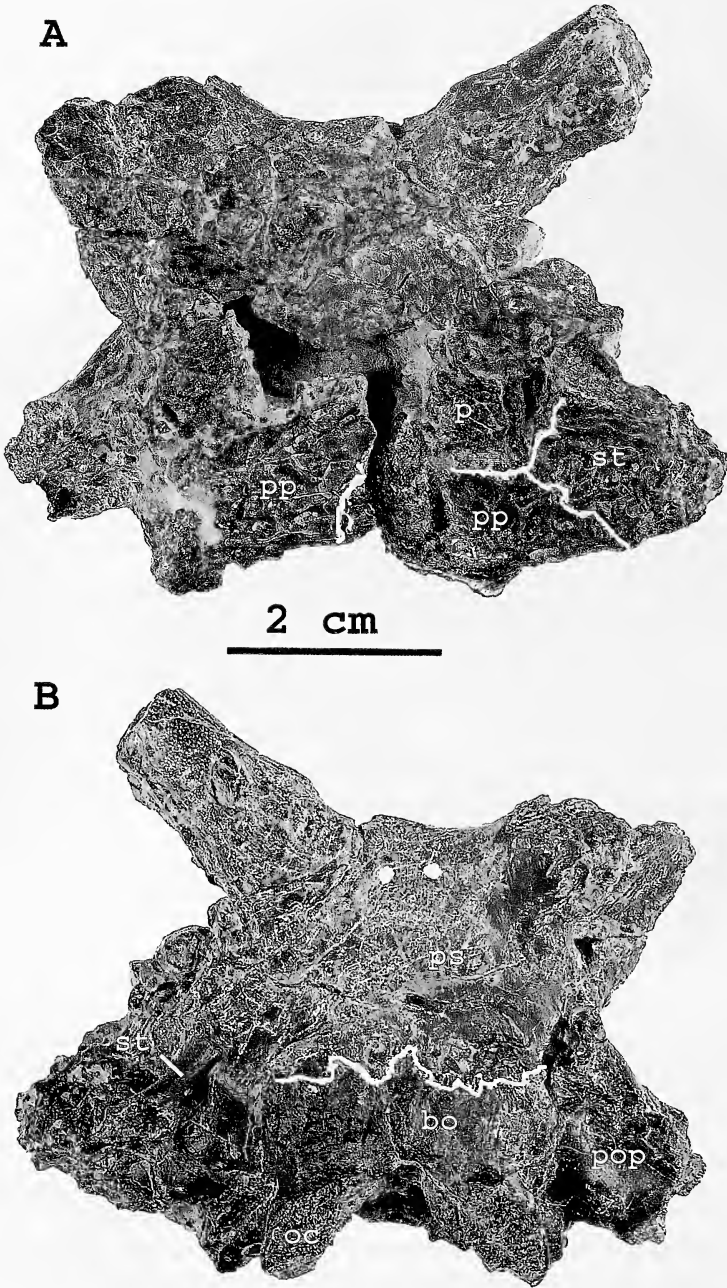


Fig. 5.—*Aspidosaurus binasser*, holotype, TMM 43531-1. Braincase in A, dorsal view with remnants of dorsal covering of dermal bones, and B, ventral view.

is a longitudinally elongate, elliptical opening, which has been referred to as either the median rostral fontanel or the internarial fenestra (Carroll, 1964; Dilkes, 1993). The more complete right nasal indicates that the anterior third of its lateral margin formed the medial margin of the external naris. Breaks have freed the anterior third of the right nasal, revealing

that its ventral surface lacks any sign of a nasal flange, which in trematopids projects ventrally from the internal surfaces of mainly the nasal and prefrontal (Dilkes, 1993). Only the anterior ends of the frontals are preserved. Their anterior margins converge on the midline to penetrate moderately between the nasals to a level well anterior of the orbits and equal to the anterior extent of the prefrontals. The right frontal indicates it had a substantial contribution to the orbital rim.

The more complete right lacrimal, lacking only minor amounts of its lateral margin, indicates a large element that is subequal in length to the nasal. Although its precise margins are not traceable, it undoubtedly had an outline of an elongated diamond, with a greatest width at its midlength, and extended from a narrow contribution to the anterior margin of the orbit to its formation of the posterolateral margin of the external naris. Of the narrow strip of the skull roof that extends from the orbit to nearly the distal end of the posterolateral, horn-like extension of the skull table and includes the postfrontal, postorbital, squamosal, supratemporal, and tabular (Fig. 4A–C), only the postorbital is nearly complete. Importantly, the elements of this strip of bone exhibit a sutural pattern and define the dorsal margin of a deep otic notch with a slight downturning posteriorly that are characteristic of dissorophoids. Unfortunately, their contribution to the narrow band of smooth bone marginal to the dorsal rim of the otic notch, the supratympanic flange, is nearly completely lost.

Only the right maxilla is essentially complete and preserved articulated with the anterior portion of the skull. Its moderate contribution to the central area of the lateral narial rim is well defined, but much of its mid-length contact with the lacrimal is only intermittently traceable due to the loss of bone. Posteriorly the maxilla, including its dentition, extends to a level just beyond the anterior margin of the orbit. Here it is widely separated from the orbital margin by its contacts with the anterior ends of first a probable, dorsal exposure of the palatine and then the jugal. The right maxilla possesses 33 teeth, or rather mostly their bases or alveoli, as only two teeth are nearly complete, and they are identical to those of the premaxilla. Anteriorly the teeth are equal in size to the largest of those of the premaxilla, judging from their basal diameter, and exhibit only a small, general decrease in size at the posterior end of the series. There is no indication of anterior “caniniform” teeth. A sculptured element with a narrowly diamond-shaped outline extends a short distance anteriorly from the anteroventral margin of the orbit and is interposed between the lacrimal medially and the jugal and maxilla laterally, and it is tentatively identified as a dorsal exposure of the palatine. The jugal is represented only by the anterior end of the right element. It obviously formed nearly the entire ventral rim of the orbit before wedging between the distal ends of the probable palatine and maxilla.

Only the right external naris is completely defined by its marginal elements. It is unusually large, with a broad, anteroposteriorly elongate oval outline. The edges of the medial and posterior narial borders formed by the nasal and lacrimal are unusual in being beveled ventrally to form a sharp edge that appears slightly serrated due to the dorsal surface sculpturing. The anterior half of the external naris is floored partially by the incomplete vomer, whereas the posterior half opens over the anterior third of the internal naris. Lying on the dorsal surface of the vomer at the anterior margin of the internal naris is an incompletely preserved septomaxilla. In its preserved position it would have divided the external naris subequally. There is no triangular, lateral projection of the narial margin of the nasal or a slight dorsal elevation of the narial margin of the maxilla that would have partially subdivided the external naris opening into two distinct portions, as in the dissorophid *Ecolsonia* (Berman et al., 1985) and trematopids (Dilkes, 1990, 1993). Although the postparietal and tabular bones overlying the braincase are incomplete, they indicate the absence of a prominent, sculptured ridge along their occipital margin. However, both elements possess portions of a narrow, smooth occipital flange.

A string of about ten, variously complete, partially overlapping, narrowly rectangular, well-ossified plates, extending from just inside the right orbit and across the posterior end of the lacrimal, undoubtedly represents a sclerotic ring. Although the possession of this structure is not unexpected in the armored dissorophids, its presence in *Aspidosaurus binasser* may represent the only irrefutable example for the group. Carroll (1964) figured a faint ring of plates in a specimen he referred to *Conjunctio*, but A. R. Milner (personal communication) reports being unable to confirm the presence of this structure in his examination of the specimen.

Although much of the palate remains, the sutures are not traceable, except for possibly that separating the right ectopterygoid and pterygoid. This is due to an expansive, dense, coarse shagreen covering of denticles that attain a maximum basal diameter of about 1 mm, particularly along the medial margin of the internal naris, and an indurate, limy, matrix surrounding their bases that cannot be removed without damage to the specimen. The internal naris is extraordinarily long, with a length equal to about three times its width. Its medial margin is greatly thickened into a dorsally curving, low, lip-like structure. Although the margins of the interpterygoid vacuities are incomplete, it is obvious that these openings were greatly expanded to the same extent as seen in other dissorophids, such as *Dissorophus*, *Broiliellus*, and *Ecolsonia* (Carroll, 1964; DeMar, 1968; Berman et al., 1985). In *Aspidosaurus binasser*, however, the vacuities appear less extensive anteriorly than in other dissorophids. This is a perception due to a lengthening of the palatal area anterior to the vacuities, including the internal nares, that reflects the unique feature in *Aspidosaurus* among dissorophids of a proportionally longer preorbital region of the skull (see "Comparisons and Discussion" section below). Scattered throughout the area of the interpterygoid vacuities are thin, irregular, denticulated plates. They are interpreted as having once formed a continuous, ossified, denticulated "skin" covering of the interpterygoid vacuity region of the palate. An identical structure was reported (Berman and Berman, 1975) in the dissorophid *Broiliellus hektotopos*, whereas an ossified "skin" membrane covering the entire palate was described (Carroll, 1964) in the amphibamid *Amphibamus lyelli*.

The anterior portions of the vomers are incomplete, but at the anteromedial margin of the right internal naris, which almost certainly was formed by the vomer, is a very large, circular alveolus that is about two-thirds occupied by the base of a large tooth and a socket. A large tooth is also present at the posteromedial margin of the internal naris that was undoubtedly borne by the palatine.

Braincase.—The nearly complete braincase of *Aspidosaurus binasser* (Fig. 5) exhibits moderate dorsoventral crushing and numerous fractures, but is well enough preserved to describe its general features and to recognize a few obvious differences from those of some medium- to large-sized dissorophids. Although all that remains of the parasphenoidal rostrum or cultriform process is a small portion (a little over 3 cm long) near its distal end, it is distinct from the thin, vertical, blade-like structure described in some dissorophids (Carroll, 1964; DeMar, 1968; Berman et al., 1981, 1985). In cross-section it has the general appearance of a stoutly constructed I-beam in which a short, stout vertical pillar separates narrowly two horizontal bars: a broad, ventral or palatal bar and a narrower dorsal bar that may have contacted the skull roof. All but the palatal bar may represent the sphenethmoid, and the channels formed on either side of the vertical pillar probably carried the olfactory nerves.

The main, posterior body of the parasphenoid has the form of large, smooth, subrectangular plate that underlies most of the anterior portion of the endochondral braincase. The stout, subcircular, rod-like structure of the basipterygoid processes is continued by the basal or internal processes of the pterygoid, with which it is solidly united by a strongly interdigitating suture to form an immobile union between the braincase and

palate. The foramina for the internal carotids are clearly visible near the midline between the basiptyergoid processes. Posterior to the basiptyergoid processes the lateral margins of the parasphenoidal plate are angled dorsolaterally to give it a slightly waisted appearance as they form the ventral margin of the fenestra ovalis. The posterolateral corners of the parasphenoidal plate are thickened slightly into a low ridge to form the cristae ventrolaterales, whereas between the cristae the posterior margin of the plate thins to a feathered edge. The basioccipital, which is co-ossified with the exoccipitals, extends well beyond the posterior margin of the parasphenoidal plate and forms, at least in part with the exoccipitals, a distinctly double occipital condyle.

In occipital view the slightly horizontally oval, concave articular surface of each condyle faces posteromedially and slightly ventrally. The exoccipital portions of the complex extend dorsally above the condyles as stout, slightly waisted processes on either side of the foramen magnum, with the basioccipital presumably making a small contribution to the ventral margin of the foramen. Dorsally the exoccipitals do not meet, but contact the occipital flanges of the postparietals, which completed the dorsal margin of the foramen magnum.

The prootic and opisthotic are co-ossified to form a single otic bone, which in *Aspidosaurus binasser* is well exposed only on the left side of the braincase. The lateral surface of the otic bone is dominated by a stout, pillar-like ridge on both the fore and aft margins of the large fenestra ovalis and extends anterodorsally onto the ventral base of the distally incomplete, flat, plate-like paroccipital process. A thin, nearly vertical, anterolaterally directed flange is co-ossified with and occupies the angle between a thickened extension of the anterior surface of the otic bone and the dorsal surface of the basicranial union. Although the dorsal and anterior margins of the flange are incomplete, its dorsal extent suggests a contact with ventral surface of the parietal, whereas anteriorly it may have contacted the transverse portion of the pterygoid. The position and extent of the flange match that described and identified as the epiptyergoid by DeMar (1968) and Schoch (1999) in *Dissorophus* and *Kamacops*, respectively. All that remains of the stapes is the expanded footplate and approximately the proximal half of the shaft of the right, which is directed posterolaterally from the fenestra ovalis. There is a gradual narrowing of the footplate to the shaft, followed by gradual but lesser expansion of the dorsal margin of the shaft. At about the neck between the footplate and shaft a foramen for the stapedia artery pierces the posteromedial surface of the stapes.

Lower Jaw.—The lower jaw in *Aspidosaurus binasser* is represented by the right mandible anterior to the adductor fossa, which is tightly joined in its correct position to the skull, whereas all that remains of the left mandible are two large, isolated segments, one including the symphysis and the other from an area anterior to the adductor fossa. Where the sutures are preserved and visible, they do not deviate from the expected dissorophid pattern. Sutures separating the coronoids, of which there were probably three, cannot be discerned, as they are covered by a continuous field of a coarse shagreen of small denticles whose bases are surrounded by an indurate limy matrix. With the exception of two complete teeth, all that remains of the marginal dentition are tooth bases, but the complete teeth duplicate in size and structure those of the upper jaw. The tooth row extends to approximately the level of the midlength of the orbit, but a tooth count is not possible.

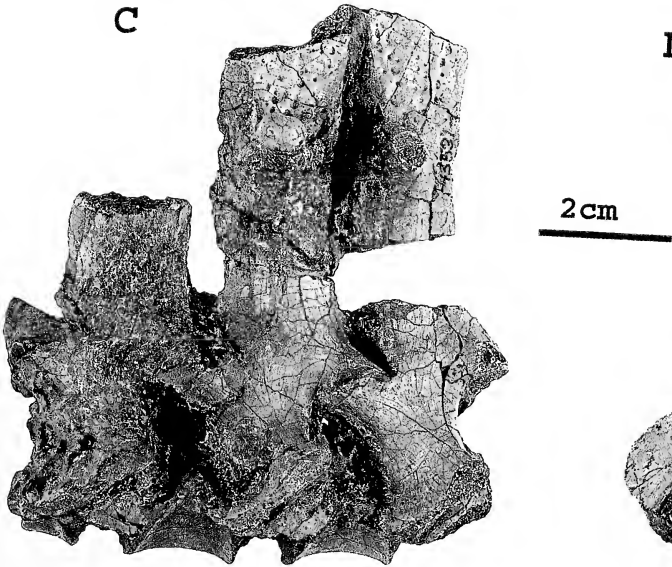
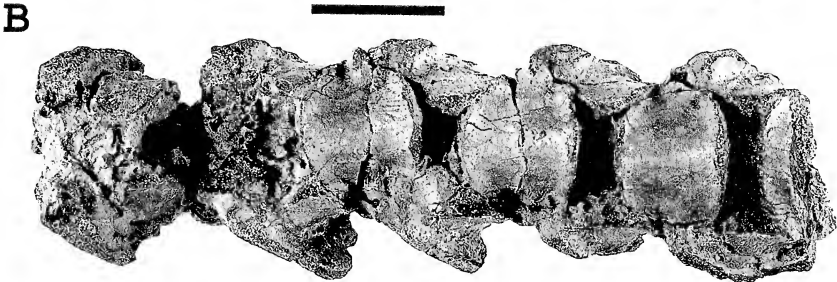
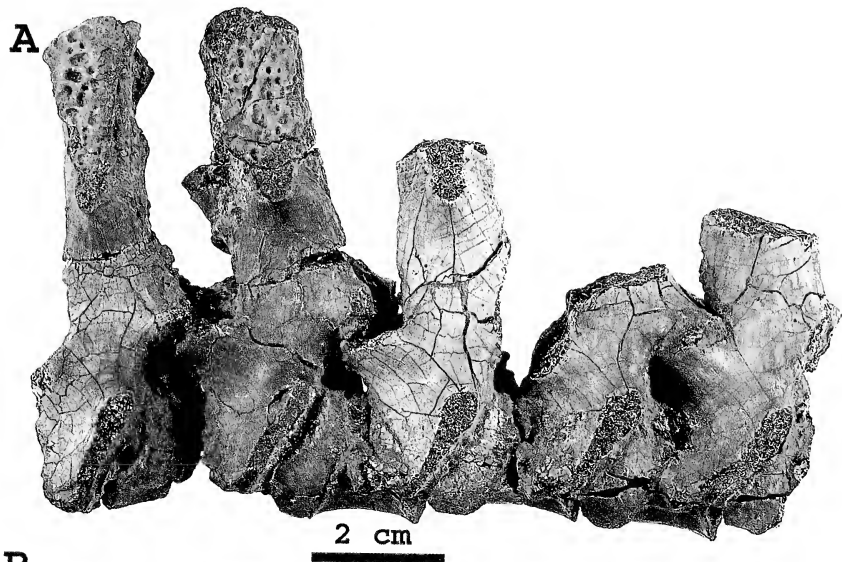
Vertebral Column.—The vertebral column is represented primarily by six short strings of from 2 to 5 closely articulated vertebrae, almost all of which lack complete neural spines. Their regional positions within the column cannot be identified beyond the conservative determinations of presacrals and caudals. In addition, there are numerous isolated vertebral elements and fragments, particularly neural spines, presumably from all regions of the column. Judging from this assortment it can be confidently estimated that the presacral

count must have at least slightly exceeded 20. The preserved central elements (Fig. 6), which are of the typical temnospondyl pattern, exhibit no marked or apparent regional differentiation other than size. They are well ossified and fit tightly together, indicating only a very minimum of intervening cartilage. However, mid-ventrally the successive intercentra are well separated from each other by ventromedial expansions of the paired, rhomboidal pleurocentra, which in lateral view appear to nearly reach the ventral margin. These spatial relationships of the central elements may be slightly exaggerated as the result of moderate, dorsoventral compression of the column. Internal ossification of the central elements is also pronounced, so that the notochordal and neural canals are expanded only moderately beyond the limits of the structures they carried. On the lateral surface of the apices of the wedge-shaped intercentrum there is typically a small, rounded, laterally projecting parapophysis. The pleurocentra support the posteroventral margins of the neural arch pedicle while contacting the intercentrum of the next posterior centrum. A short, anteroventrally elongate transverse process projects laterally from very near the entire posteroventral margin of the neural arch pedicle, terminating as the diapophysis. Its distal end is very slightly beveled ventromedially so that the articular surface, which narrows noticeably ventrally, faces laterally and slightly ventrally. The articular planes of the well-developed zygapophyses slope strongly ventromedially.

Dermal armor fused to the distal ends of neural spines is present in all of the preserved neural spines of *A. binasser* that are complete enough to detect its presence. The armored neural spines are remarkable for their wide range in morphology, particularly the dermal-armor portion. To avoid confusion the terms "armored neural spine" or simply "spine" are used here to refer to combined, fused elements of the endochondral neural spine of the neural arch and the sculptured, plate or segment of dermal bone widely referred to as armor. For the convenience of description three types of armored neural spines are recognized: **type 1**, dermal armor roof-shaped and neural spine with prominent, bilaterally paired tubercles (Fig. 6); **type 2**, dermal armor roof-shaped and neural spine lacks lateral tubercles (Fig. 7); and **type 3**, laterally compressed to an extremely thin spatulate-shaped structure and neural spine with prominent, bilaterally paired tubercles (Fig. 8). Type 1 is the most common of the preserved armored neural spines, with a minimum number of examples approximately 35 and, therefore, must have dominated most regions of the column. They are represented in the short, articulated strings of the largest preserved vertebrae that are presumably from the presacral region of the column (Fig. 6), but most occur as isolated, much smaller fragments. In general, the dermal armor segment capping the neural spine is roof-shaped, with each half of the roof sloping steeply ventrolaterally from a keel-like crest whose midline length is equal to or slightly greater than the anteroposterior width of the neural spine summit. The ventrolaterally sloping halves of the roof form a ventral, midsagittal angle between them of about 40°, and each ends ventrally at about the mid-height of the spine in a V-shaped border. The external surface of the dermal cap is strongly sculptured by a reticulate pattern of ridges surrounding deep, irregular pits except for a distinct, smooth area that is finely pitted along the anterior and posterior margins near its summit. In anterior or posterior view the distal portion of the neural spine is expanded

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Fig. 6.—*Aspidosaurus binasser*, holotype, TMM 43531-1. Presumed presacral vertebrae possessing armored neural spines referred to in the text as being of the "type 1" morphology in which the dermal armor is roof-shaped and the neural spine possesses prominent, bilaterally paired tubercles. A, left lateral, and B, ventral views of five incomplete, articulated vertebrae in which only the armored neural spine of the anteriormost vertebra is complete. C, left lateral, and D, anterior views of three incomplete, articulated vertebrae, with the latter view showing the full lateral extent of the paired tubercles of the second element of the series.



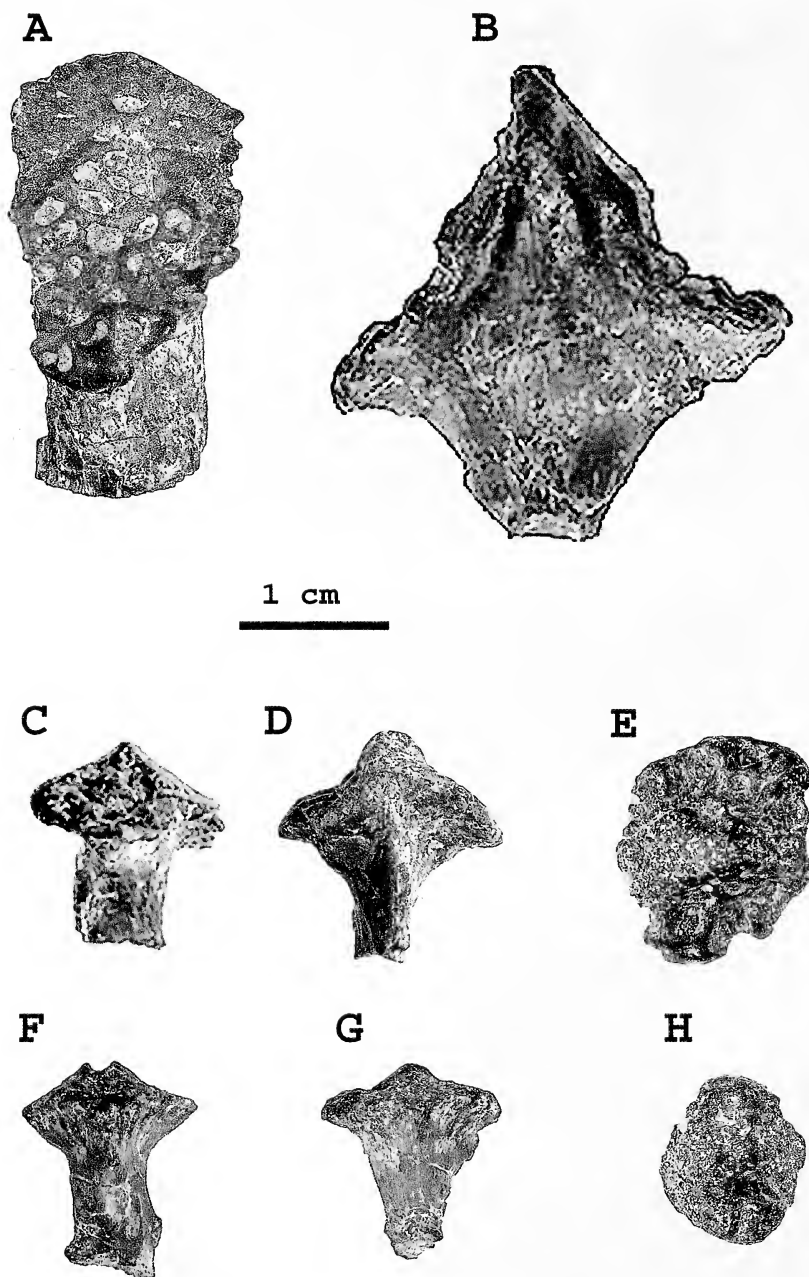
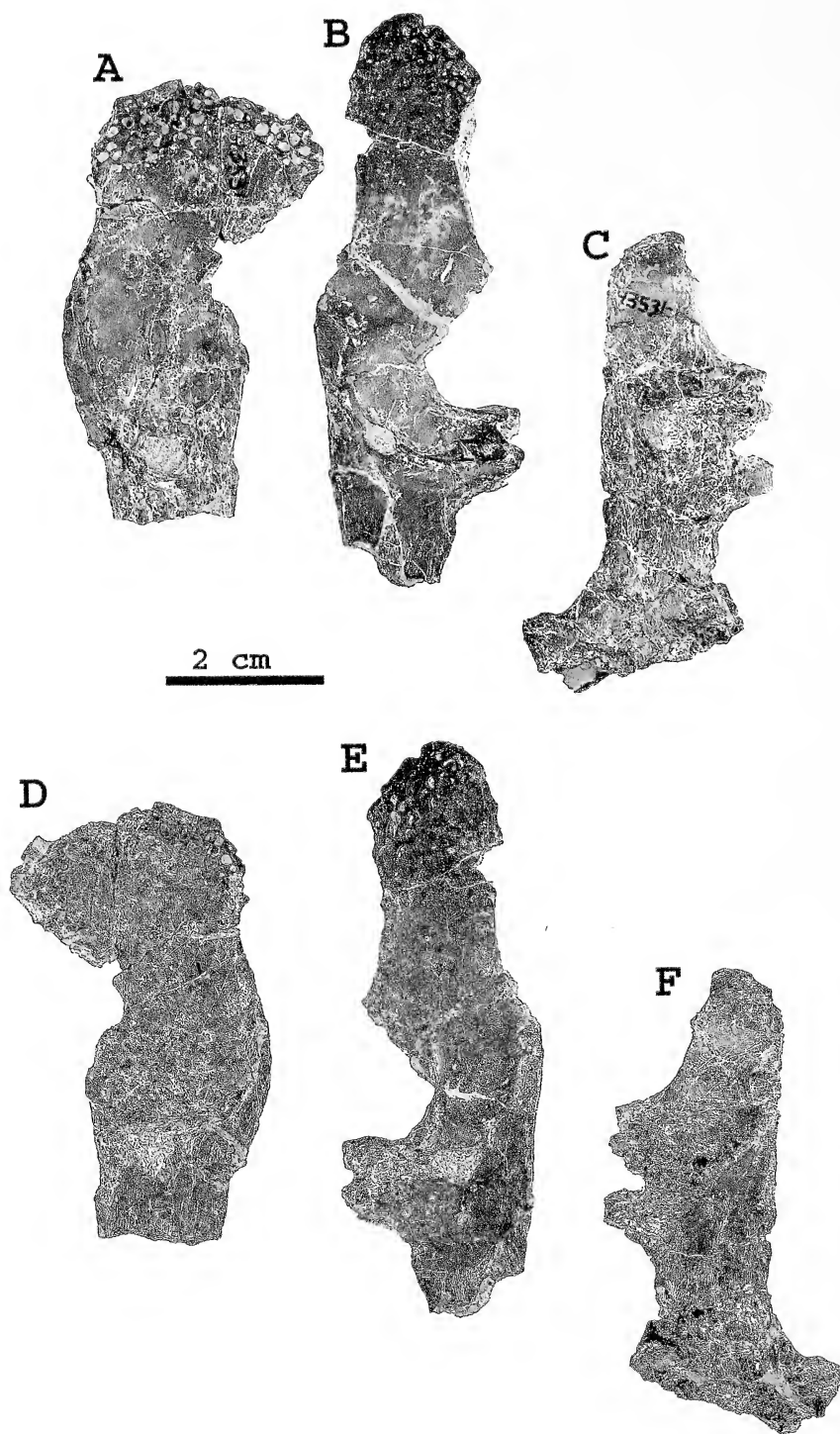


Fig. 7.—*Aspidosaurus binasser*, holotype TMM 43531-1. Armored, vertebral neural spines referred to in the text as being of the “type 2” morphology in which the dermal armor is in general roof-shaped but quite variable in overall structure and the neural spine lacks lateral tubercles. A, lateral, and B, longitudinal views, respectively, of an armored neural spine having the form of a steeply pitched, roof-shaped structure. C and F, D and G, and E and H, lateral, longitudinal, and dorsal views, respectively, of two armored neural spines having the form of a mushroom-like structure.

laterally to fuse with the inner margins of the dermal armor cap, and then narrows to a normal width below the dermal cap so as to have an overall outline of a vertically elongated diamond. In the same views a strongly developed, median ridge at the level of the capping armor is continued ventrally as the edge of the neural spine. On both sides of the neural spine the ventral, V-shaped termination of the dermal armored segment is marked by a strongly developed, laterally projecting, cylindrical tubercle, often broken off, that appears to originate from the neural spine at about its midheight. However, the ventral apex of the sculptured dermal cap is continued onto the dorsal surface of the lateral tubercle. The paired, lateral tubercles of each neural spine are bilaterally positioned, and those of successive neural spines in the articulated examples are aligned along the column so as to occupy a single horizontal plane. The heights of the type 1 armored neural spines appear quite typical compared to other temnospondyls and do not vary noticeably along the column.

Examples of the type 2 armored neural spine (Fig. 7), having generally roof-shaped dermal armor and no obvious development of lateral tubercles, are the least represented, with about 10 examples. All are fragmentary, having been broken off the neural arch above the zygapophysis, and exhibit a considerable range in size and morphology, with the diminutive size of some indicating a far distal position in the tail. In one variant (Fig. 7A, B) the lateral halves of the deeply sculptured roof-shaped dermal cap diverge from one another ventrolaterally in the form of an inverted V, with a midsagittal ventral angle between them of about 70°. The roof-shaped dermal cap sometimes expands a short distance beyond the anterior and posterior margins of the neural spine, giving them a slightly greater length longitudinally relative to their lateral width than in the type 1 spine. However, as in the type 1 spine, the dorsal surface is strongly sculptured except for a smooth, very finely pitted area along the anterior and posterior margins that expands toward the midline crest. Considering the large size of this variant of the type 2 armored neural spine, it could be from either the presacral or the anterior caudal region of the column. In a second, very small variant (Fig. 7C–H) the dermal cap is circular to subcircular in dorsal outline, and its dorsal surface varies from slightly dome-shaped to very slightly roof-shaped, giving it a mushroom-like appearance. Again, the dorsal surface is coarsely sculptured except for a smooth, very finely pitted area along the anterior and posterior margins that expands toward the midline crest.

The laterally compressed, extremely thin, spatulate-shaped type 3 armored neural spines are very distinct from those described above. Of the type 3 spines there are perhaps as many as a dozen examples, mostly fragments, but three (Fig. 8) are represented by all but a small portion of the base of the neural spine. Fortunately, one of the spines (Fig. 8C, F) is complete enough to include most of the zygapophyses, and thus provides clues to the anterior-posterior orientations of the other two examples. Immediately noticeable is that the spines are extremely compressed laterally to form tall, thin blades of variable dimensions, but in general expand gradually distally into a convex distal margin. Clearly, those in Figure 8 suggest a greatest spine height perhaps equaling twice that of the presacral type 1 spines. Their thinness is due apparently in great part to the neural spine only partially penetrating distally between the lateral halves of the dermal cap and not being expanded. The sculpturing of the spine is most accentuated along the distal convex margin. On either side of the spine the lower portion of the sculpturing ends ventrally by its fore and aft margins, both marked by a prominent ridge, converging on a well-developed lateral tubercle that is broken off at the base in all the examples at hand. Again, the paired tubercles are bilaterally positioned and appear to have their origin mainly from the neural spine. At or just above the level of the lateral tubercle the posterior margin of the spine exhibits a deep, smooth, concave embayment, whereas the anterior margin may vary from slightly convex to straight. The ventral margin of the embayment may be extended posteriorly by a stout,



pronounced protuberance that is thickened into a rounded cross-section with a papillose-like lateral sculpturing of smoothly finished bone and a deeply, irregularly pitted posterior surface of unfinished bone. Undoubtedly, this structure served as the site of attachment of a thick band of interspinal ligaments. In the most complete of the type 3 spines, the one that includes the zygapophyses (Fig. 8C, F), there is a second, much smaller, posteriorly projecting process just below the prominent posterior protuberance. Its smoothly rounded ventral margin forms a second, larger, broadly concave embayment before bifurcating to form buttresses to the posterior zygapophyses. In the type 3 spine there are no smooth areas along the anterior and posterior margins of the lateral, sculptured surfaces of the spine, as in the spine types 1 and 2. Instead, the anterior and posterior edges of the spine are typically indented in the form of a narrow, shallow channel of unfinished bone that undoubtedly represents an area of attachment of interspinal ligaments. Compared to the type 1 spines believed to be from the presacral region of the column, in the type 3 spines the bases of the neural spines are much thinner in cross-section and the pre- and postzygapophyses are set much closer to the midline, suggesting that they represent anterior caudals. Furthermore, they are extremely variable size, as might be expected if anterior caudals, which in amphibians typically exhibit a pronounced decrease in size posteriorly.

Associated with some of the articulated vertebral material are ribs with prominent uncinate processes, which is a typical feature of dissorophids.

COMPARISONS AND DISCUSSION

Despite the incompleteness and unavailability for study of the holotype of *Aspidosaurus chiton*, Broili's (1904) description, including figures of the skull and numerous vertebrae, is sufficient to assure the validity of the species and its assignment to Dissorophidae. Although additional specimens of *Aspidosaurus* have since been described, they are based on very small portions of vertebral column. This is unfortunate, as Broili's description of the skull of *A. chiton* was somewhat superficial, and thus eliminates a possible detailed comparison with the holotypic skull of *A. binasser*.

Broili's (1904) description and illustration of the skull of *Aspidosaurus chiton* does reveal, however, several features that are not only present in *A. binasser*, but when considered collectively also provide convincing evidence of dissorophid affinities: 1) skull outline broadly triangular with a broadly rounded snout; 2) large, circular orbits; 3) large external naris with a broad, anteroposterior elongate oval outline; 4) deep, prominent otic notch; 5) thickening of the prefrontal and postorbital bones into broadly rounded, anteroposteriorly oriented, ridge-like swellings that become broader and thicker toward the orbital rim; 6) pit-and-ridge sculpturing strongly accentuated along the margins of the skull table and the postorbital cheek region; 7) ossified denticulated 'skin' covering of the interpterygoid vacuity region of the palate; and 8) marginal teeth small, closely set, sharply pointed, and slightly recurved. Although Broili (1904) did not indicate whether *A. chiton* possessed extremely wide interpterygoid vacuities, which is typical of all dissorophids, including *A. binasser*, it almost certainly would have possessed this feature.

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Fig. 8.—*Aspidosaurus binasser*, holotype TMM 43531-1. Armored neural spines of presumed anterior caudal vertebrae referred to in the text as being of the "type 3" morphology in which the dermal armor and neural spine form of a thin, laterally compressed, spatulate-shaped structure and possess paired, bilaterally paired tubercles. A, B, and C, left lateral views and D, E, and F, right lateral views of the same three armored neural spines, respectively. Orientation can be confirmed only in the spine of C and D, as it includes the zygapophyses. The spines are aligned with their lateral tubercles (broken off at their bases except in F) at the same plane.

Most importantly, Broili's (1904) illustration of the skull of *A. chiton* reveals one easily recognizable feature that is shared with *A. binasser* and distinguishes both from all other dissorophids: a greater preorbital length of the skull. Measurements made from Broili's illustration of the skull of *A. chiton* in dorsal view yield the following rough estimates: midline skull length, 8.0 cm; preorbital length, 4.1 cm; postorbital length to the distal end of tabular, 3.0 cm. These measurements indicate a preorbital length that is about 51% of the skull length and significantly greater than the postorbital length. In *A. binasser* the same three skull measurements, 19.5, 10.5, and 7.0 cm, respectively, indicate a preorbital length that is about 54% of the skull length and significantly greater than the postorbital length. The range of available measurements for other dissorophids, on the other hand, indicates a preorbital length that is about 35–45% of the skull length and subequal or, more typically, shorter than the postorbital length (DeMar, 1968; Berman et al., 1981, 1985). A striking feature of *A. binasser* among Lower Permian forms is the large size of its skull (Bolt, 1974). In this feature it is approached only by *Platyhystrix*, with a midline skull length of about 19.0 cm (Berman et al., 1981).

Not being able to make direct comparison with the holotype of *A. chiton* also eliminates the opportunity to determine whether it possessed any of the following cranial features that collectively distinguish *A. binasser* from other dissorophids: 1) possession of an internarial fenestra or median rostral fontanel; 2) dorsal exposure of the palatine on the skull roof; 3) internal naris extremely long, with a length equal to about three times its width; and 4) basiptyergoid process of the braincase and the basal process of pterygoid firmly united suturally to produce an immobile basicranial articulation. Similarly, it is unknown whether *A. chiton* possessed any of the following characters that uniquely distinguish *A. binasser* from all other dissorophids: 1) maxilla and its dentition end posteriorly at a level just posterior to anterior orbital margin, rather than extending farther posteriorly to a level at or a short distance beyond the posterior orbital margin; 2) nasal and lacrimal margins of the external naris beveled ventrally to a sharp edge, with the dorsal surface sculpturing giving them a serrated appearance; 3) frontals extend anteriorly to a level well beyond the anterior orbital margins and equal to the anterior extent of the prefrontals. Although the frontals in dissorophids may extend a short distance beyond the level of the orbits, they never reach the level of the anterior extent of the prefrontals; 4) jugal extends anteriorly to approximately the level of the anterior margin of the orbit, rather than ending at about the midlength of the orbit; and 5) presence of an anterior palatal fenestra. Considering the very conservative nature to cranial differentiation displayed between members of the same dissorophid genus, it is likely that most of both sets of the above cranial features would be expected to be present in *A. chiton*.

Although cranial comparisons offer no definitive means for distinguishing between the holotypes of *Aspidosaurus binasser* and *A. chiton*, the vertebrae do. However, this avenue of comparison has been complicated somewhat by the descriptions of three additional species of *Aspidosaurus*, all based on very small, fragmentary, postcranial specimens from Lower Permian deposits in Texas and New Mexico that consist mainly or solely of vertebrae exhibiting the distinctive, structural pattern of the armored neural spines in *A. chiton*: *A. glascoeki* Case, 1910, represented only by the holotype (AMNH 4864), consisting of five articulate vertebrae with armor from the Lower Permian Petrolia Formation (ex Belle Plains, Hentz, 1988), Wichita Group, of Texas (Romer, 1928); *A. (Zatrachys) apicalis* (Cope, 1878), represented only by the holotype (AMNH 4785), consisting of the distal ends of several neural spines with armor from the Lower Permian Abo Formation of New Mexico; and *A. (Zatrachys) crucifer* (Case, 1903), represented not only by the holotype, a single neural spine with armor (CNHM UC 1205) for which there is no exact stratigraphic or locality data other than Lower Permian of Texas, but also several

specimens of isolated vertebrae with armor assigned to it from various levels in the Lower Permian of Texas (DeMar 1966; Carroll, 1964). Generic reassignment of the latter two species was made by Case (1910), who realized the erroneous association of *Aspidosaurus* vertebrae with cranial material of *Zatrachys*. Case (1911) and DeMar (1966) have presented excellent illustrations and descriptions that succinctly detail the differences between their armored neural spines of all three species, which reasonably explains why the validity of all three taxa has been accepted for so long. It is now evident, however, that the differences between them are not sufficient for species identification, but rather are easily accounted for by the wide range of variation of the armored neural spines in *A. chiton* and *A. binasser*. It should also be noted here that *Aspidosaurus* obviously does not include *A. novomexicanus*, originally described by Williston (1911), and Langston's (1953) reassignment of the species to the dissorophid *Broiliellus* on the basis of referred specimens is widely accepted (DeMar, 1966).

Although the sample size of the armored neural spines available to Broili (1904) in describing *A. chiton* may have been somewhat limited, two or possibly three types can be recognized as essentially duplicating those in other previously described species of *Aspidosaurus*. His generalized reconstruction of two articulated vertebrae with slightly overlapping, roof-shaped armor segments, which he believed may have come from the anterior presacral region or possibly the sacral region of the column, has apparently been widely accepted as typifying the entire column by most (Case, 1911; DeMar, 1966) but not all (Carroll, 1964) later authors. They are not significantly different, however, from those seen in the holotype of *A. glascocki*, which have been described as coarsely sculptured, roof-shaped dermal armor plates firmly fused to the expanded dorsal ends of neural spines that not only overlap each other anteriorly and posteriorly in no particular order, but also appear to be partly fused at their overlapping margins. Also among the armored spines of *A. chiton* illustrated by Broili (1904) are those resembling *A. crucifer*, which are also identical to those described here as type 2 in *A. binasser*. The holotypic armored neural spines of *A. apicalis* (now lost according to DeMar, 1966), which were described (Case, 1911; DeMar, 1966) as coarsely sculptured, flat, oval in dorsal outline, with a median dorsal keel, approach those in *A. crucifer* and described here as a variant of type 2 in *A. binasser*. Considering the above similarities and the wide range of variation in the armored spines in *A. chiton* and especially *A. binasser*, the very fragmentary holotypes on which *A. glascocki*, *A. apicalis*, and *A. crucifer* are based must be considered as an insufficient grounds for specific identification, and so the three species are regarded here as *nomina dubia*. On the other hand, the occurrence of neural spines with overlapping dermal armor in *A. chiton* but not in *A. binasser*, and the absence in *A. chiton* of armored spines that in *A. binasser* are described here as types 1 (dermal armor roof-shaped and neural spine with prominent, bilaterally paired tubercles) and 3 (laterally compressed to extremely thin, spatulate-shaped structure and neural spine with prominent, bilaterally paired tubercles) provides a firm basis for recognizing both species as valid. It is also worth noting that despite specific differences in their armored neural spines, the holotype of *A. binasser* confirms the association of the skull and vertebrae attributed by Broili (1904) to *A. chiton*.

It has been suggested (DeMar, 1966) that the finely pitted, smooth areas bordering the anterior and posterior margins on the dorsal surface of the otherwise coarsely sculptured dermal armor in *Aspidosaurus* may indicate an area of overlap by a second, more superficial segmental series of dermal ossifications, termed the "external series" by DeMar (1966), which did not contact the vertebral column, but rather alternated with the series capping the neural spines. However, among all of the vertebral material at hand there are no dermal armor segments that could be interpreted as representing this second, external series of segmental armor. In light of this, a more reasonable interpretation of these smooth, finely

pitted areas bordering the anterior and posterior margins of the dermal armor is that they represent areas of attachment of interspinal ligaments that functioned to strengthen the vertebral column. In none of the vertebral central materials of *Aspidosaurus binasser* that might be interpreted as caudals is there evidence of fusion, as has been reported (DeMar, 1968) in the dissorophid *Dissorophus multicinctus*.

In describing the wide range of variation of the armored spines in *Aspidosaurus*, DeMar (1966) and Carroll (1964) believed that some exhibited an overlap in morphology with the type represented by the Early Permian *Platyhystrix*. Considering the unique, bizarre, armored neural spines in *Platyhystrix*, as well as those of the rare, very closely related Pennsylvanian *Astreptorhachis*, whose spines are like those in *Platyhystrix* except for fusion between consecutive neural arches and spines (Vaughn, 1971), the likelihood of confusion seems very improbable, but it has occurred. The armored neural spines of *Platyhystrix* are greatly elongated, strongly compressed laterally, and expanded gradually distally in the sagittal plane, and except for a short proximal portion, they exhibit a presumed dermal covering of exuberant, nodular sculpturing. Furthermore, as pointed out by Vaughn (1971), the sculpturing of the armor in *Aspidosaurus* tends to form anastomosing ridges separated by large, deep pits, whereas that in *Platyhystrix* differs in having large tubercle-like protuberances that tend to be separate. Furthermore, an articulated series of *Platyhystrix* presacral vertebrae illustrated by Lewis and Vaughn (1965) showed clearly that in lateral view the spines formed a greatly expanded, sail-like structure with a strongly convex dorsal edge that is somewhat analogous to that in some pelycosaurian-grade synapsids. DeMar's (1966) precautionary statement of possible confusion between the two genera was based on a single specimen (MCZ 1258) of *Aspidosaurus* that consisted of several articulated neural spines with dermal armor assigned to *A. crucifer*. Of the four armored neural spines described and illustrated by DeMar (1966; fig. 7), two conformed exactly to the *Aspidosaurus* pattern, but he believed two approached the pattern of *Platyhystrix* in exhibiting a greater dorsal extension of the armored portion of the neural spine and with little lateral expansion, and in one of these the armor extended a short distance posterior to the neural spine with a continuation of the sculpturing on its posterior margin. By way of comparison with *A. binasser*, this is a minor deviation at best and should not be confused with the very distinct pattern in *Platyhystrix*. As a second example of confusion, Carroll (1964; pl. 1) illustrated eight, isolated armored neural spines (MCZ 1477) from the Lower Permian of Texas that he believed aptly demonstrated a transition in form between those observed in *A. chiton* and *Platyhystrix*. It is now clear that two of these, the long-spines examples on the left and right margins of his plate 1, belong to *Platyhystrix*, whereas three of the six shorter-spined examples are of the *Aspidosaurus* "crucifer" type, and all that can be said of the remaining three is that they belong to *Aspidosaurus*.

It is worth emphasizing that the presacral vertebrae of *A. binasser* were of moderate, subequal height and did not form a sail-like structure as in *Platyhystrix*. However, the spatulate-shaped, type 3 spines believed to be possibly from the caudal region in *A. binasser* are not only slight higher than those of the presacral region, but also are variable in height, suggesting the possibility of a moderate-sized, sail-like structure in the anterior region of the tail. It is also likely that the presacral column in *A. binasser* contained more vertebral segments than in *Platyhystrix*. It is roughly estimated that the presacral portion of the column in *A. binasser* contained 20 or more vertebrae, which is in line with temnospondyls in general and counts 21 to 25 in other dissorophids (Carroll, 1964; DeMar, 1968), but is in marked contrast to an estimated count of 15 or fewer in *Platyhystrix* (Lewis and Vaughn, 1965).

The supposed similarity between the vertebrae of *Aspidosaurus* and *Platyhystrix* has prompted speculations that they were closely related and perhaps formed a distinct lineage

within the Dissorophidae. In a phylogeny of the Dissorophidae, Carroll (1964) showed *Platyhystrix* as an offshoot of the *Aspidosaurus* assemblage, and, furthermore, suggested that the *Aspidosaurus*-*Platyhystrix* assemblage separated from the remainder of the dissorophids late in the Pennsylvanian or in the Early Permian. On the basis of similar structural patterns of the armored neural spines in Dissorophidae, DeMar (1966) recognized two major groupings, the Dissorophinae that includes *Dissorophus* and *Broiliellus* and the Aspidosaurinae that includes *Cacops*, *Aspidosaurus* and *Alegeinosaurus*. The description of *Aspidosaurus binasser* has provided for the first time details of the skull of a member of that genus and the opportunity to compare it with the single description (Berman et al., 1981) of the skull in *Platyhystrix*. Without enumerating numerous structural and proportional differences, the comparison would seem to dispel any speculation of a close relationship between *Aspidosaurus* and *Platyhystrix*.

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FROM THE ARCHIVES AND COLLECTIONS

W. J. HOLLAND'S INSTRUCTIONS TO C. V. HARTMAN FOR
THE 1903 COSTA RICA EXPEDITIONDAVID R. WATTERS¹OSCAR FONSECA ZAMORA²

THE CONTEXT OF THE LETTER

Director William Jacob Holland provided this letter to Carl Vilhelm Hartman on March 24, 1903, only seven days after he reported for duty at Carnegie Museum. He had been hired as Curator of the Section of Ethnology and Archaeology on February 28, one month after applying for the position, and was to take up that post not later than March 15, although he actually reported for duty two days later (Watters and Fonseca Zamora, 2001*b*). In his negotiations and correspondence with Holland, Hartman had emphasized his knowledge of collections of antiquities available for purchase, his personal contacts with influential persons, and his desire to resume archaeological fieldwork in Costa Rica (Watters and Fonseca Zamora, 2002*a*:280–282).

Holland regarded this situation as an ideal opportunity for the young Carnegie Museum to acquire, quickly, impressive Costa Rican antiquities for the future exhibits being planned for the expanded Carnegie Institute facility to open in 1907. Hartman, knowing of the director's desire, pressed for the swift purchase of the Velasco collection, then "on deposit" at a Philadelphia museum, though its owner, Padre José María Velasco, resided in Costa Rica. He stressed the urgency of the matter by alerting Holland that competing institutions were aware of this collection's availability.

This strategy was successful. The Director started making arrangements for the expedition by writing letters to Costa Rican and American government agencies on March 16, the day before Hartman arrived. During the next week, Holland composed four letters to influential individuals in Costa Rica; he gave them to Hartman to hand-deliver when they met on March 24. Hartman left Pittsburgh by train on March 25, the day after receiving the instructions; by March 27 he was in New Orleans, aboard the steamship *Preston* for the voyage to Puerto Limón, Costa Rica (Watters and Fonseca Zamora, 2003:111).

THE CONTENT OF THE LETTER

The original two-page letter of instructions, typed double-spaced, is reproduced below in its entirety. It is edited for minor points, such as inserting a bracketed comma to clarify text and a bracketed *sic* to signify a typographical or grammatical error. Holland used no diacritical marks in the original and we follow that convention in this version.

¹ Curator, Section of Anthropology.

² Research Associate, Section of Anthropology (and Professor, retired, University of Costa Rica).
Submitted 8 August 2003.

March 24, 1903

Mr. C. V. Hartman,
Curator of Ethnology in the Carnegie Museum

Dear Sir,—

In confirmation of the instructions orally given you I desire hereby to say to you, that it is my wish as Director of the Museum that you proceed to Costa Rica for the purpose of prosecuting, on behalf of this Museum, researches in natural history, and more especially in relation to the ethnology and archaeology of that country.

Having understood from you that Mons[ieur]. Pittier de Fabrego [sic], the Director of the National Museum of Costa Rica, at San Jose, has [sic] expressed his willingness to make an arrangement with you to undertake the arrangement of the archaeological collections of the institution to some extent at least, and has proposed to you that in return for such services and in return for exchanges of North America material to be given to the Costa Rica Museum[,] he will cause a set of the duplicate materials in that institution to be transferred and set over to this institution, I hereby request you to make arrangements with the Director of the National Museum in Costa Rica having in view the consummation of such a plan, and you are authorized for a period of at least three months to tender your services to the Director of the National Museum in Costa Rica. Should a longer period be required than this[,] arrangements may be made on conference with me by letter.

You are also requested if possible to make arrangements to secure for this Museum at the lowest price at which you can secure the same—not to exceed the sum of three thousand dollars unless otherwise authorized by letter—the collection of Costa Rican antiquities belonging to Don Jose Maria Velasco of Santa Cruz, Costa Rica, now in the temporary custody of the University of Pennsylvania in Philadelphia.

I shall be pleased if you are able to carry out some independent investigations leading to the acquisition of desirable ethnological and archaeological material for this Museum, on the lines suggested to me in your communication of March the 23d, which is before me, and incidentally[,] if you are able[,] to make collections of botanical, entomological and other specimens.

I expect you to keep me thoroughly informed by letter of your movements and your plans.

An outfit consisting of photographic material, tent, etc., has been provided, and you will be expected to return the same to the institution after you are through with it.

I entrust to you the sum of five hundred dollars, for which, together with any other sum that may hereafter be entrusted to you, I shall expect you to render to me a fully itemized account, as required by the rules of the institution.

I am, with assurance of highest esteem and regard,

Very respectfully yours,

Director Carnegie Museum

[Letter of instructions, W. J. Holland to C. V. Hartman, March 24, 1903, Holland Letter Book, 1903, pages 162–163]

THE SIGNIFICANCE OF THE LETTER

Hartman first proposed a Carnegie Museum expedition in his initial letter to Holland, dated January 28, 1903, and its scope was determined during their negotiations for his employment as Curator (Watters and Fonseca Zamora, 2001*b*). Holland already was aware of Hartman's important archaeological expedition to Costa Rica in 1896–1897 for the Swedish Society for Anthropology and Geography and the Royal Museum of Natural History (Watters and Fonseca Zamora, 2002*a*:266–267, 272, 279–280, 2002*b*). He first met Hartman at the 13th Session of the International Congress of Americanists (13th ICA) in 1902 and heard his lecture about the earlier Costa Rican research. He was in the audience when it was announced that Hartman had received the prestigious Duc de Loubat Prize for his impressive book about the expedition. Holland also made the acquaintance of the Costa Rican representatives, Henri Pittier de Fábrega and Juan Fernández Ferraz, at the 13th ICA (Watters, 2002). Thus, Holland was predisposed to a proposal for a Carnegie Museum expedition, given his knowledge of Hartman's extensive experience in Costa Rica. In fact, his familiarity with the country was one of the primary reasons for his employment at Carnegie Museum (Watters and Fonseca Zamora, 2001*b*).

Holland moved swiftly to organize the expedition, and the scope of preparations is impressive (see Appendix). He wrote to Señor J. B. Calvo at the Costa Rican legation in

Washington, D.C. to discuss the expedition and ask for letters of introduction, which he received in a response letter written three days later. He contacted John Hay, Secretary of State for the United States, to obtain letters of introduction to the American minister and consuls resident in Costa Rica. On March 21, Holland wrote a letter and a draft agreement to Padre Velasco, both composed in Spanish, about Hartman's trip and the purchase of the collection in Philadelphia. Two days later he wrote to Señor Leonidas Pacheco, Secretary of Public Instruction, whose name had been provided by Calvo, and to his two acquaintances from the 13th ICA the year before, Henri Pittier de Fábrega, Director of the Instituto Físico-Geográfico (IFG), and Juan Fernández Ferraz. The letter of instructions was the final item of preparatory correspondence. Therein he mentions a written communication received from Hartman on March 23, a document that, in view of its content, unfortunately has not been found in either the Hartman or Holland Archives at Carnegie Museum of Natural History.

Holland also arranged for the outfitting of the expedition, fulfilling Hartman's requests for a photographic camera and supplies, a tent and hammock, and other field gear. His assistant, Douglas Stewart, reserved the train and steamship tickets, although Hartman's letter from the *Preston* discloses that not everything went smoothly (see Appendix). By the final time they met, on March 24, Holland had composed the written instructions that were to direct Hartman's efforts in Costa Rica on behalf of Carnegie Museum. Holland had organized the entire expedition in just over one week.

In the first paragraph of the instructions, Holland set out the general guidelines for the expedition, directing Hartman to conduct research in natural history in general and more specifically studies in ethnology and archaeology. Later in the letter he asked him to collect, as feasible, botanical, entomological, and other specimens. Since Hartman was educated as a botanist before he changed his career to anthropology, and Holland was a highly respected entomologist, the request for those collections was reasonable.

The second paragraph referred to an arrangement between Hartman and Pittier de Fábrega for research at the Museo Nacional de Costa Rica (MNCR). Hartman, in his initial letter to Holland on January 28, spoke of Pittier de Fábrega's desire to have him return to Costa Rica to arrange and classify the MNCR archaeological collections. He also informed Holland that Pittier de Fábrega, in charge of the IFG, had "affiliated" the MNCR after Juan Fernández Ferraz was discharged as its director. Who actually headed the MNCR in 1903–1904 is a confusing issue (Watters and Fonseca Zamora, 2002a:285). Holland refers to Pittier de Fábrega as the MNCR director in the letter of instructions, but he used the IFG address on his March 23 letter of introduction (see Appendix). Señor Calvo listed Pittier de Fábrega as IFG Director, yet Holland referred to him as MNCR Director in his March 30 thank-you letter to Calvo. Kandler's (1987:28) history of the MNCR stated that Fernández Ferraz served as director until 1904, in contradiction to Hartman's statement that he had been discharged in 1903. Holland addressed his March 23 letter to Fernández Ferraz simply using San José, Costa Rica, without specifying a title or an institution, and he made no reference to the museum within that letter, implying that he regarded Fernández Ferraz as no longer being in charge. Garrón de Doryan (1974:54–55) stated that Anastasio Alfaro resumed directorship of the MNCR in 1904 (he headed the institution from 1887 until 1898, when Fernández Ferraz replaced him). Regardless of who actually was in charge of the MNCR during the 1903 expedition, though we believe the weight of evidence better supports Pittier de Fábrega's directorship, the arrangements outlined in the second paragraph are of particular interest.

The MNCR was expected to transfer to Carnegie Museum a set of its duplicate materials in return for Hartman's service of "... at least three months ..." to arrange its archaeological collections. Carnegie Museum in return was willing to exchange North

American materials, and a list of available entomological, ornithological, mineralogical, and ethnological specimens (see Appendix) was produced, presumably by Holland, for Hartman to take to the MNCR. Hartman indeed spent about three months at the MNCR, working intermittently in San José between field trips to sites in the Highlands, Atlantic plain, and Pacific coast, and he extensively photographed its holdings for comparative purposes.

The third paragraph charged Hartman with acquiring the Velasco collection of antiquities "... now in the temporary custody ..." of the museum in Philadelphia. Holland instructed Hartman to secure this collection at the lowest price, not to exceed \$3000. On April 18, he notified the Director that the collection in Philadelphia as well as a second collection assembled by Velasco, this one in Costa Rica, had been obtained for a total sum of \$2200 (Watters and Fonseca Zamora, 2003:111–112).

The next paragraph mentioned very generally the "independent investigations" to be carried out by Hartman because they were detailed in his March 23 communication (the missing document). He apparently proposed both ethnographic and archaeological projects, although his fieldwork ended up being almost exclusively at archaeological sites. He did secure certain natural history specimens in line with the Director's wishes. Table 1 presents the anthropological and natural history collections obtained by Hartman for Carnegie Museum.

The final three paragraphs dealt with procedural matters, keeping the Director informed, returning the field outfit provided, and accounting for expedition monies with which Hartman was entrusted.

The March 24 letter of instructions provides insight into Holland's management style. In the first paragraph, the Director directed Hartman to proceed with the expedition on behalf of Carnegie Museum and specified the kinds of research to be undertaken. In the next two paragraphs he "requests," though these are more in the form of directives, that Hartman carry through with the approved plans to work at the MNCR and purchase the Velasco collection. In the first case Holland set a time limit of about three months, although a longer period may be authorized after consultation with the Director. In the second instance he placed an upper limit on the amount available for expenditure unless the Director authorized otherwise by letter. The Director expected to be kept informed of Hartman's activities and required, per institution policy, a fully itemized accounting of expenses. The letter's text gives the impression that Holland retained overall control of the expedition, delegated limited authority to Hartman and only for specific tasks, and expected to be consulted when needed. Control really was relinquished only in paragraph four, concerning the independent investigations, where Hartman was given some leeway in determining his field research, although even then it was to be carried out "... along the lines ..." suggested to the Director in the written communication of March 23.

Hartman documented his perspective on the March 24 meeting in a letter he wrote four years later, to C. C. Mellor, Chair of the Museum Committee, in which he expressed his disappointment about the Director's "... severe condition ..." with regard to allowable field living expenses (Watters and Fonseca Zamora, 2003:111). At that meeting Holland told Hartman to submit reports, on a monthly basis, accounting for expenses and detailing his activities. This requirement became an increasing problem as the expedition progressed. Despite routine written requests from Holland, Hartman failed to account for expenses until June, after almost three months in Costa Rica, and when he submitted the report it contained items subsequently disallowed by Holland. In November, after Hartman had returned to Carnegie Museum, he met with the Director to try to resolve the expense issues. The letter to Mellor makes it clear that the "resolution" was not satisfactory to Hartman (Watters and Fonseca Zamora, 2003:126).

Table 1.—Annual Report records of Costa Rican anthropological artifacts and natural history specimens obtained by C. V. Hartman for Carnegie Museum¹.

Accession/Annual report ²	Description	Remarks
2300 AR 1904:48	Collection of Costa Rican moths	Staff Collection by Hartman
2314 AR 1904:48	Lepidoptera from Costa Rica (2 small boxes)	Staff Collection by Hartman
2386 AR 1904:53	Herbarium specimens from Costa Rica	Exchange, Instituto Physico-Geographico [sic], probably arranged by Hartman
2424 AR 1904:48	Ten fresh-water Decapods (6 <i>Palaeamon</i> , 4 <i>Atya</i>) ³ from Río de Colón, Costa Rica	Staff Collection by Hartman
2437 AR 1904:53	Velasco collection of Costa Rican antiquities	Purchased by Trustees, from José María Velasco, San José [Santa Cruz], Costa Rica
2438 AR 1904:53	Velasco collection of Costa Rican antiquities	Purchased by Trustees, from José María Velasco, San José [Santa Cruz], Costa Rica
2439 AR 1904:53	Troyo collection of Costa Rican antiquities	Purchased by Trustees, from Estate of Juan Troyo [José Ramón Rojas Troyo], San José [Cartago], Costa Rica
2440 AR 1904:48	Collection of antiquities made in Costa Rica	Staff Collection by Hartman
2595 AR 1905:49	Land shells collected at Las Guacas, near Nicoya, Costa Rica	Staff Collection by Hartman
2597 AR 1905:49	One specimen of Liverwort collected in Costa Rica	Staff Collection by Hartman
2690 AR 1905:49	Scorpion with eighty-seven young, captured at Alajuela, Costa Rica	Staff Collection by Hartman
2749 AR 1905:49	Tapir skull from Las Guacas, Nicoya, Costa Rica	Staff Collection by Hartman
2792 AR 1906:58	Collection of Costa Rican antiquities	Purchased by Trustees, from Dr. Juan Fernández Ferraz, San José, Costa Rica
2793 AR 1906:55	Archaeological collections from Costa Rica	Staff Collection by Hartman
2939 AR 1906:59	Collection of antiquities from Nicoya, Costa Rica	Purchased by Trustees, from El Presbítero Señor Don José Velasco, Santa Cruz, Costa Rica
3272 AR 1908:61	Three species of shells (<i>Pteria</i> , <i>Arca</i> and <i>Melongena</i>). Collected in Gulf of Nicoya, Costa Rica	Gift from C. V. Hartman
3519 AR 1909:65	Two mats of "iule" from Pacaca, Costa Rica, made by the Indians	Purchased by Trustees, from C. V. Hartman
3520 AR 1909:65	Marimba (musical implement) from the pueblo of Nicoya	Purchased by Trustees, from C. V. Hartman
3521 AR 1909:65	Collection of modern pottery from Costa Rica (46 pieces)	Purchased by Trustees, from Professor H. Pittier de Fábrega, National Museum, San José, Costa Rica
3522 AR 1909:65	Indian skulls (12) from the stone cist graves in the district of Cartago, Costa Rica	Purchased by Trustees, from C. V. Hartman
3523 AR 1909:65	Six vessels of the <i>Crescentia</i> fruit (tree calabash), San José, Costa Rica	Purchased by Trustees, from C. V. Hartman
3524 AR 1909:65	Coffee Basket from Costa Rica	Purchased by Trustees, from C. V. Hartman
3743 AR 1909:65	Archaeological collection of 24 clay and stone objects from Cartago, Costa Rica	Purchased by Trustees, from C. V. Hartman

¹ Excludes specimens collected by Hartman in Pennsylvania (Accession #2575 and #2586) and exchanges he arranged with Naturhistoriska Riksmuseet, Stockholm, Sweden (#3798), Yale University Museum (#4290), and American Museum of Natural History (#4291).

² The annual report year ended on March 31 (e.g., AR 1904 covers period from April 1, 1903 to March 31, 1904).

³ Taxon nomenclature is as originally recorded in the relevant annual report.

The duration of the expedition likewise caused friction. Holland's agreement to at least three months referred specifically to the collaborative work at the MNCR; the fieldwork at archaeological sites required an additional commitment of time. Hartman generally kept the Director apprised of his activities in a series of letters, although they were not in the "monthly report" format Holland had requested. He was able to secure the Director's approval for extensions to the project, first to August, then September, and finally through October, but it is clear that toward the end of the expedition Holland had major reservations about just what was being accomplished. On November 12, Hartman cabled from New Orleans, stating that the steamship from Limón had been delayed and he would take the first train available to Pittsburgh. In all, Hartman had been in Costa Rica about seven and a half months.

Holland wrote two reports on the preparations for the Costa Rica expedition. In the *Annual Report of the Director for the Year Ending March 31, 1903*, after reporting Hartman's employment, Holland wrote:

Mr. Hartman, acting under the instruction of the Director, after conference with him, has been deputed to make some further investigations in the Central American countries, with a view to the acquisition by this Museum of material illustrative of the ancient Aztec civilizaton [sic], as well as the natural history of these countries (Holland, 1903a:24).

By using "Central American countries," this report implied that an expedition broader in geographic scope might have been considered at one time. Such a project would have been in line with the idea of fieldwork within "Spanish America" discussed by Holland and Hartman (Watters and Fonseca Zamora, 2003:110, 123). It also would have been more in accord with Hartman's first expedition (1896–1899) to Central America for the Swedish institutions, when he conducted archaeological research in Costa Rica and ethnographic research in El Salvador and Guatemala (Watters and Fonseca Zamora, 2002a:266–267, 2002b). Since the *Annual Report* year ended March 31, a month after Hartman was employed and just a few days after he departed for Costa Rica, Holland might have prepared this statement ahead of time, before a broader scale project was pared down to the work in Costa Rica alone. Holland certainly was wrong in referencing the ancient Aztec civilization in this report.

The second document is Holland's Monthly Report, prepared for the meeting of the Museum Committee on Tuesday, March 31, 1903. It provides greater detail about some aspects of the project, allows us to extrapolate Hartman's sailing date from New Orleans, and corroborates information about the preparations for the expedition known from other sources (see Appendix). Holland wrote:

Mr. C. V. Hartman reported for duty on the 17th inst. Feeling that it is of the highest importance that he shall as soon as possible endeavor to negotiate for the purchase of the collection [Velasco collection in Philadelphia] concerning which I spoke at the last meeting, I dispatched him to Costa Rica. I procured for him letters of introduction from the Secretary of State and from the minister of Costa Rica in Washington, His Excellency Bernardo Calvo. He called for an outfit consisting of [a] tent and hammock and a good photographic camera, and these articles I supplied to him. The bills for the same are included in the account. I advanced to him the sum of five hundred dollars on account of his expenses, purchasing for this purpose American Express Company checks, upon which there is a charge of \$2.50. He sailed last Friday [March 27] from New Orleans, and in a letter received [from the *Preston*] he expresses

considerable anxiety lest two representatives of the National Museum whom he found on board should be on the same errand bent. It is to be hoped that this is not the case. I gave him a lengthy letter of instructions, and hope that the result of this brief excursion will be the acquisition of much valuable and needed material (Holland, 1903*b*).

In this communication with the Museum Committee, Holland emphasized the importance of acquiring collections, the aspect of the expedition that in his view clearly was the most significant element for Carnegie Museum (Watters and Fonseca Zamora, 2003:134). The attached "Accounts Due and Payable March 31st 1903" document detailed the costs incurred in outfitting the expedition—W. Howard Morrison, photography outfit (\$180.80) and supplies (\$28.56); Mاماux & Son, tent, hammock, etc. (\$30.00); railroad and steamship fare from Pittsburgh to Limón (\$81.35); and cash advanced to Hartman (\$502.50). This document does not identify the camera make and model, a vexing omission in view of the many glass-plate negative images Hartman left to Carnegie Museum illustrating his fieldwork and the artifacts studied at the MNCR in 1903 (Watters and Fonseca Zamora, 2001*a*, 2002*a*:292–293).

Holland's careful preparations for the 1903 Costa Rica expedition paid important dividends for Carnegie Museum. Hartman provided the institution with major archaeological collections, both purchased and excavated, as well as smaller ethnographic and natural history collections (Table 1). Through exchanges of Costa Rican artifacts with other museums, Carnegie Museum obtained materials from areas of the world (Peru, West Indies, Panama, and New Guinea) poorly represented in its collections. The fieldwork generated the first monograph on archaeology published in the Carnegie Museum *Memoirs* series, as well as two articles in journals (Hartman, 1907*a*, 1907*b*, 1910). Hartman raised awareness of Carnegie Museum's expedition among museum personnel and anthropologists, through presentations at the International Congress of Americanists and American Anthropological Association, and during visits for comparative research with colleagues at other museums. For Holland, however, the greatest dividend of the expedition undoubtedly was the prominent position held by the Costa Rican artifacts in the exhibits in the Gallery of Archaeology, when his vision of a new Carnegie Museum came to fruition with the opening of the expanded Carnegie Institute facility in 1907.

ACKNOWLEDGMENTS

We express our sincere gratitude to the Adrienne and Milton Porter Charitable Foundation for a grant allowing us to study the Holland and Hartman Archives at Carnegie Museum of Natural History. The interplay between Hartman and Holland, which ranged from collegial to contentious, is an intriguing element of our investigation into Carnegie Museum's early history. Anthropology Collection Manager Deborah G. Harding and Librarian Bernadette Callery helped us to resolve certain confusing issues regarding the Hartman accessions.

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APPENDIX

Preparatory correspondence for the 1903 expedition

- Holland to Señor Don Joaquín Bernardo Calvo, Envoy Extraordinary and Minister Plenipotentiary of Costa Rica in Washington, D. C., March 16 [Holland Letter Book, 1903, pages 124–125]
 - informs Calvo of the planned expedition and outlines Hartman's credentials
 - requests "...letters of introduction to scientific gentlemen connected with your government, and particularly to the Minister of Public Instruction."
- Holland to Mr. John Hay, Secretary of State of the United States, Washington, D. C., March 16 [Holland Letter Book, 1903, page 126]
 - informs Hay of the planned expedition and outlines Hartman's credentials
 - requests letters of introduction to the "... American minister and to any of the consuls who may be resident there [in Costa Rica] ..."
- J. B. Calvo, Legación de Costa Rica en Washington, to Holland, March 19 (in English) [Section of Anthropology, C. V. Hartman Donor File]
 - responds to Holland's letter of March 16
 - includes letters of introduction for Hartman to deliver to Señor Pacheco, the Secretary of Public Instruction, and Professor Pittier, Director of the Instituto Físico-Geográfico
- Holland to Señor Presbítero Don José María Velasco, Santa Cruz, Costa Rica, March 21, with an attached draft agreement (both in Spanish) [Holland Letter Book, 1903, pages 149–150] [diacritical marks omitted by Holland have been inserted herein]
 - informs Velasco that the "... representante del Museo Carnegie el administrador del departamento [sic] etnológico Sr. Don Carlos F. [sic] Hartman ..." will be conducting various natural history studies in Costa Rica
 - requests that Velasco attend to Hartman were he to have the opportunity to revisit Guanacaste province
 - the draft agreement proposes to purchase from Velasco his "... colección de antigüedades de Costa Rica, al presente depositada en el Museo de la Universidad de Pennsylvania en la ciudad de Philadelphia ..."
- Holland to Professor H. Pittier [de Fábrega], Director del Instituto Físico-Geográfico, San José, Costa Rica, March 23 [Holland Letter Book, 1903, page 159]
 - informs Pittier that Hartman, with whom "You already are well acquainted ..." is now serving as Curator of Ethnology at Carnegie Museum
 - solicits Pittier's assistance in Hartman's work in Costa Rica
 - Holland recalls with great pleasure having made Pittier's acquaintance "... at the recent Congress of Americanists and on the occasion of your visit to Pittsburgh ..."

6. List of material which may be promised in return for material from the Costa Rican Museum (undated document) [Holland Letter Book, 1903, page 161]
 - lists entomological, ornithological, mineralogical, and ethnological collections available for exchange by Carnegie Museum
 - probably accompanied Holland's March 23 letter to Pittier
7. Holland to Dr. Juan F[ernández]. Ferraz, San José, Costa Rica, March 23 [Holland Letter Book, 1903, page 152]
 - Holland indicates Fernández Ferraz needs "... no introduction to our mutual friend Hartman ..."
 - informs him that Hartman, now serving as Curator of Ethnology and Archaeology at Carnegie Museum, is "... returning to Costa Rica to conduct some researches in natural history and to continue his investigations as to the antiquities of your country."
 - solicits "Any kindness which you may show him ..."
 - Holland recalls "... our meeting both in New York and Pittsburgh during the recent sessions of the Congress of Americanists ..."
8. Holland to Señor Lic. Don Leonidas Pacheco, Secretaría de Instrucción Pública, San José, Costa Rica, March 23 (in English) [Holland Letter Book, 1903, page 158]
 - letter of introduction recommending Hartman to Pacheco and informing him of the purposes of the visit
 - states "Professor Hartman is already acquainted with Costa Rica and is the author of a work upon the antiquities of that country ..."
 - solicits Pacheco's "... kindest consideration, and hope that you may be able to smoothe [sic] before him his path as an investigator."
9. Hartman to Douglas Stewart, from the United Fruit Company steamship *Preston* in New Orleans, March 27 [Section of Anthropology, C. V. Hartman Donor File]
 - addressed to Douglas Stewart, the Assistant in the Director's Office
 - informs Stewart that in Cincinnati he had to purchase a new ticket because the supposedly reserved ticket for a sleeper to New Orleans could not be found
 - encountered "... Dr. Cook and two other gentlemen of the Bureau of Agriculture in Washington" aboard the *Preston*
 - expresses concern that they might have been given commissions to buy Costa Rican archaeological collections by Professor Holmes (W. H. Holmes of the Bureau of American Ethnology, Smithsonian Institution)
10. Holland to His Excellency, J. B. Calvo, Legation of Costa Rica, Washington, D.C., March 30 [Holland Letter Book, 1903, page 182]
 - acknowledges Calvo's kindness in having written letters of introduction for Hartman to the Minister of Public Education and the Director of the Costa Rican National Museum (note that Calvo's March 19 letter lists Pittier as Director of the Instituto Físico-Geográfico, not the National Museum)

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